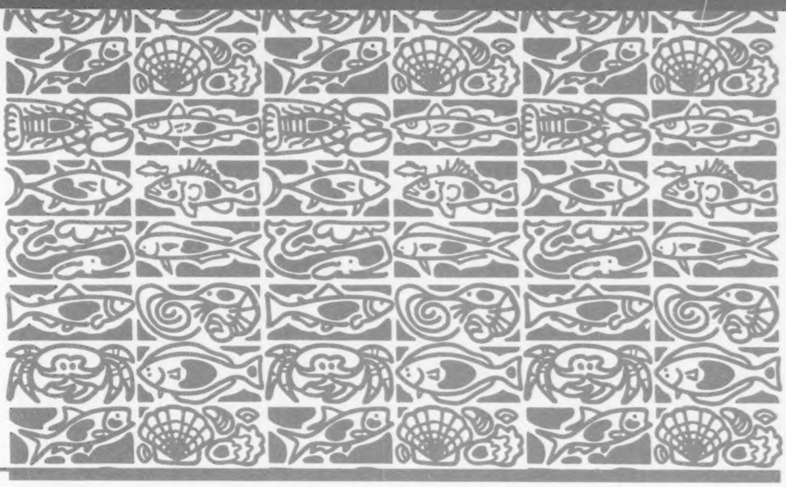

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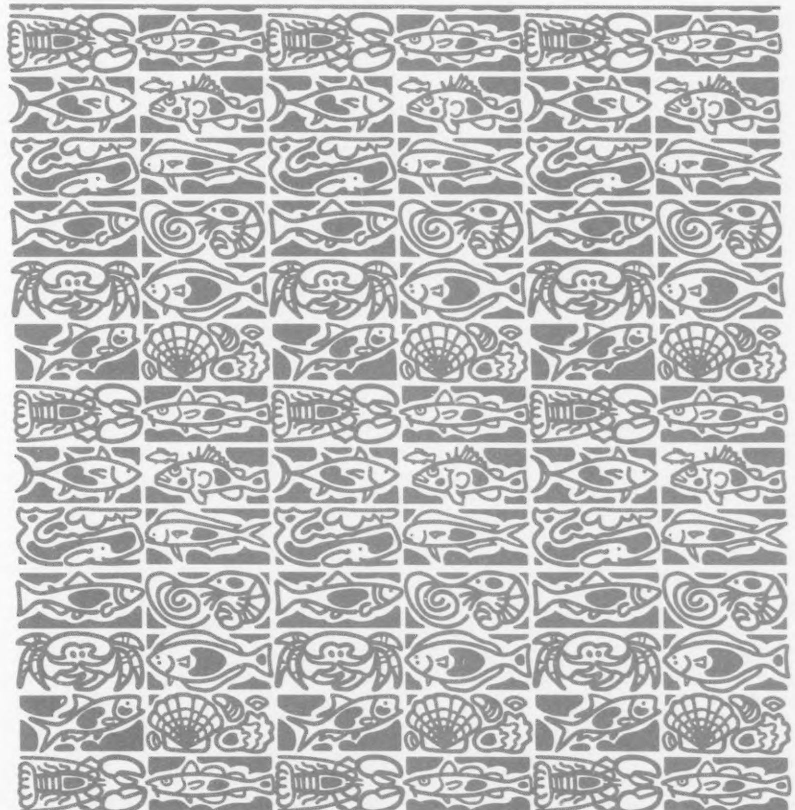

Fishery Bulletin

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Abstract—The use of parasites as indicators of the stock structure of Pacific halibut (*Hippoglossus stenolepis*) in the northeast Pacific was investigated by using 328 adult (>55 cm fork length) halibut from 15 composite localities ranging from northern California to the northern Bering Sea and 96 juvenile (10–55 cm) halibut from five localities ranging from the northern Queen Charlotte Islands to the Bering Sea. Counts of eight selected parasite species (the juvenile acanthocephalans *Corynosoma strumosum* and *C. villosum*, the metacestode *Nybelinia surmenicola*, the digenean metacercaria *Otodistomum* sp., and the larval nematodes *Anisakis simplex*, *Pseudoterranova decipiens*, *Contracaecum* sp., and Spirurid gen. sp.) that produce infections of long duration, do not multiply in the host, and that have a relatively high abundance in at least one geographic locality were subjected to discriminant function analysis. Juvenile Pacific halibut showed no separation and, even though they were not heavily infected with parasites, the analysis suggested that juveniles could be a mixed stock. Three groups of adults were identified: fish from California to the southern Queen Charlotte Islands, those from the northern Queen Charlotte Islands to the central Bering Sea, and those from the central and northern Bering Sea. These groups suggest that the single stock concept be more thoroughly evaluated.

The use of parasites in discriminating stocks of Pacific halibut (*Hippoglossus stenolepis*) in the northeast Pacific

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The Pacific halibut (*Hippoglossus stenolepis*) is an Arctic–Boreal Pacific pleuronectid flatfish ranging throughout the North Pacific from southern California to northern Japan, but is most abundant in the Gulf of Alaska. The halibut supports one of the top five commercial fisheries in North America, with average annual landings of approximately 25,000 metric tons from 1991 to 1995 (IPHC, 1996), and is also widely sought in the sport fishery, thus contributing significantly to west coast economies. The International Pacific Halibut Commission (IPHC) is responsible for management of the resource. From the 1930s through the 1950s the IPHC recognized at least three stocks of halibut from tagging experiments, egg and larval drift, anatomical differences, and differences in growth rate: 1) those in the Bering Sea; 2) those from the Gulf of Alaska south to Cape Spencer, Alaska; and 3) those south of Cape Spencer (Skud, 1977). These boundaries roughly followed the zoogeographic zonation in the North Pacific. Skud (1977) re-analyzed the data and concluded that there was extensive intermingling of fish among areas and that there was no evidence to indicate that fish north and south of Cape Spencer, Alaska, constituted different stocks. Available biochemical evidence (Tsuyuki et al., 1969; Grant et al., 1984), although limited in scope and by sampling effort, suggests little genetic variation throughout the northeast Pacific. As a result, the IPHC manages halibut as a single population, but with statistical divisions for management of data.

Parasites have been used successfully to distinguish populations or stocks of fishes and, as a result, provide information useful in fisheries management (see

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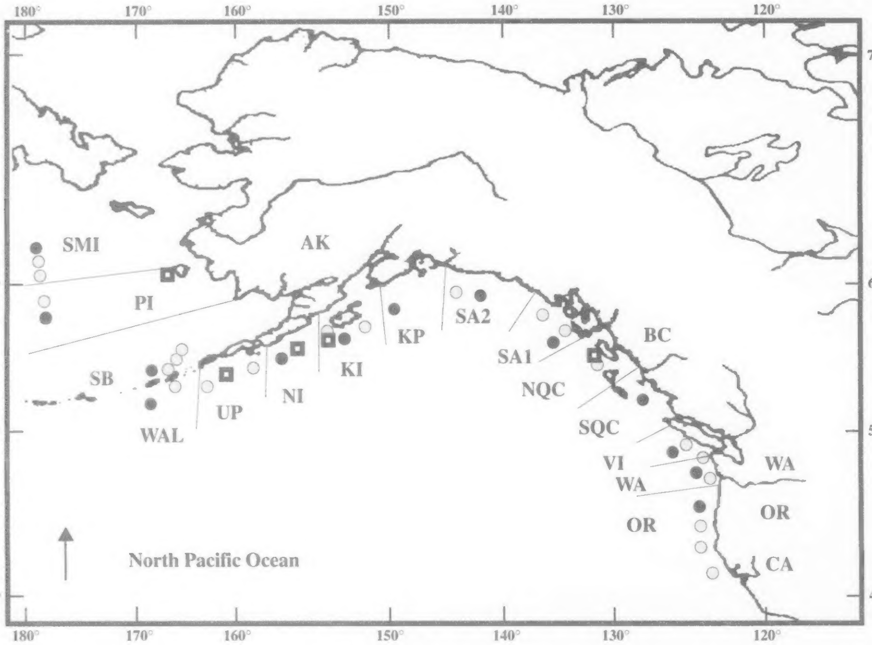

Figure 1

Sampling localities for 328 adult (circles) and 96 juvenile (squares) Pacific halibut, *Hippoglossus stenolepis*, in the northeast Pacific. OR = Oregon–northern California, WA = Washington, VI = Vancouver Island, SQC = southern Queen Charlotte Islands, NQC = northern Queen Charlotte Islands, SA1 = southeast Alaska site 1, SA2 = southeast Alaska site 2, KP = Kenai Peninsula, KI = Kodiak Island, NI = Nagai Island, UP = Unimak Pass, WAL = western Aleutian Islands, SB = southern Bering Sea, PI = Pribilof Island, SMI = St. Matthew Island. Individual hauls with at least 10 fish (for a total of 202 fish) are shown as solid circles. Other collection sites are shown as stippled circles. See Table 1 for sample sizes.

reviews by Lester, 1990; Moser, 1991; Williams et al., 1992). With respect to flatfish, Gibson (1972) used parasitological data to distinguish three groups of *Platichthys flesus* and Krzykawski and Wierzbicka (1982) used parasitological data and other information to distinguish between Barents Sea and Labrador stocks of Greenland halibut, *Reinhardtius hippoglossoides*. Khan et al. (1982) and Arthur and Albert (1993) used parasites to distinguish between Atlantic and Gulf of St. Lawrence stocks of *R. hippoglossoides*, and Boje et al. (1997) used parasites to indicate differences among Greenland stocks of Greenland halibut and stocks from the western Atlantic. No similar work on flatfishes has been done in the Pacific and, with the exception of Krzykawski and Wierzbicka (1982) and Boje et al. (1997), there has been no attempt to distinguish between stocks of a species across a significant portion of the species' range.

In this article, we use discriminant analysis on counts of some of the parasites from adult Pacific halibut to determine if they form discrete groups or stocks in the northeast Pacific. We do a similar analysis on the juvenile fish and compare the results to the adult analysis to determine when separation is likely to occur.

Materials and methods

A total of 328 adults (>55 cm fork length) from 15 composite localities, ranging from northern California to the vicinity of St. Matthew's Island in the Bering Sea and 96 juveniles (10–55 cm) from five localities ranging from the northern Queen Charlotte Islands to the Bering Sea (Fig. 1), were caught by staffs of the IPHC and the U.S. National Marine Fisheries Service during the summers of 1990–92 (using longlines and trawls). Most localities (for the adult samples) included fish taken from several hauls; however, 202 fish came from 13 individual hauls, each of which contained at least 10 fish. Fish were bagged individually and immediately frozen at sea for later examination.

Fish and parasites were processed by using standard parasitological techniques (see Blaylock et al., 1998a). We followed Bush et al.'s (1997) definitions for prevalence, abundance, and intensity. Parasites used in the analyses were chosen according to the guidelines of Arthur and Albert (1993). Only those species with infections of long duration, that do not multiply in the host, and that have a relatively high abundance in at least one geographic locality were used. Of the 59 parasite taxa identified from

Pacific halibut (Blaylock et al., 1998a), eight taxa met these criteria: the juvenile acanthocephalans *Corynosoma strumosum* (body cavity) and *C. villosum* (body cavity), the metacestode *Nybelinia surmenicola* (stomach wall), the digenean metacercaria *Otodistomum* sp. (stomach wall), and the larval nematodes *Anisakis simplex* (body cavity, organs, musculature), *Pseudoterranova decipiens* (body cavity, organs, musculature), *Contracaecum* sp.(body cavity), and Spirurid gen. sp. (stomach wall). A ninth taxon, the larval nematode *Hysterothylacium aduncum* (body cavity and organs) was included for the analysis of juveniles.

Because individual fish varied extensively in size (fork length), and the number of a parasite individuals was strongly correlated with fish size (Blaylock et al., 1998a), parasite numbers were corrected for differences in host size. Counts of individual parasites were first log-transformed ($\ln(x+1)$). To adjust for the effect of fish length, a regression of the transformed parasite numbers on fish length for each species in each locality (and haul) was calculated. This relationship was then used to adjust the number of parasite individuals within each fish in each locality (and haul) to that expected for the average-size fish in the overall sample (80.9 cm for adults, 39.2 cm for juveniles). These data were then used in discriminant function analyses. We applied the most widely used (and available) method of discriminant function analysis, in which the data were divided into training and test sets, and a discriminant function calculated on the training set was used to classify the test set. Interpretations were based on patterns in the test sets. To insure that any identified patterns were due to differences among localities rather than simply differences among individual hauls, we performed the same analysis on both the locality and the individual haul data.

Our training set consisted of six fish randomly selected from each haul ("haul" training set) or these fish plus four from the northern Queen Charlotte Islands and six from Unimak Pass ("locality" training set). Discriminant functions calculated from data on these "training" fish were used to classify each of the remaining fish from each haul ("haul" test set) or those fish plus all remaining fish ("locality" test set). The test set fish were first classified into one of the 13 hauls or 15 localities. Classification matrices were examined for the degree of misclassification. Hauls or localities were then grouped and regrouped into four and three groups based on patterns in the 13 or 15 category analyses and the zoogeographic zones from Blaylock et al. (1998b). Analyses were then repeated. Classifications were examined for misclassification, and boundaries adjusted for retesting. Results presented are those from the best fit "test" classifications. Statistical analyses were performed in SYSTAT for Windows version 5.05 (Wilkinson et al., 1992). The entire data set from which the data for this analysis came is available for purchase from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

Results

Of the taxa that met the Arthur and Albert (1993) criteria, *N. surmenicola* was most common and abundant in northern localities and fairly common and abundant in central localities. *Corynosoma strumosum*, although variable in prevalence and abundance, was much more common in the northernmost localities. *Corynosoma villosum*, although prevalent everywhere, was more abundant in northern fish. *Otodistomum* sp. and Spirurid gen. sp. were more common and abundant in southern localities. *Anisakis simplex*, although present in virtually every fish from every locality, was more abundant in southern fish. *Pseudoterranova decipiens* and *Contracaecum* sp. appeared to be more common in central areas (Table 1). In the juveniles, *A. simplex* and *P. decipiens* were more common in central localities, whereas *C. villosum*, *C. strumosum*, and *Hysterothylacium aduncum* were more common in northern localities (Table 2).

The haul analyses indicated that the majority of fish from some hauls (12/14 Vancouver Island [VI] fish, 3/4 Southeast Alaska 1 [SA1] fish, 3/5 from the Pribilof Islands [PI], and all 4 from St. Matthew's Island [SMI]) could be correctly classified but that fish from surrounding areas also were incorrectly classified to these hauls. Moreover, the percentage of fish correctly classified by the haul functions was, in all cases, within only a few percentage points of that correctly classified by the equivalent locality function. Thus, patterns do not appear to be associated with independent hauls. Therefore, we present only the results of the locality analyses.

Fifteen category discriminant analyses revealed severe misclassification in most areas. Only 39% were correctly classified to locality (Table 3). The functions did assign correctly the majority of test fish from two localities (19/26 from Vancouver Island [VI] and 14/22 from the southern Bering Sea [SB]). However, misclassification of fish from surrounding areas to these localities indicated less than accurate discrimination. The clearest indications from these analyses were that localities from the vicinity of the Queen Charlotte Islands south should be grouped together and that there is a suggestion that the two northern Bering Sea locations (PI and SMI) should be grouped.

Regrouping the localities into four categories by using boundaries from zoogeographic analyses (Blaylock et al., 1998b) plus the apparent northern Bering Sea grouping (PI–SMI), considerably improved the predictive ability of the functions. The "best fit" four-category grouping gave approximately 62% correct classification at the locality level (Table 4). The four-category functions were good predictors for the California–Oregon (OR) to southern Queen Charlotte Islands (SQC) fish; over 80% of these southern fish were correctly classified, and only about 6% of the other fish were misclassified to this group. Over 70% of the Pribilof–St. Matthew Island (PI–SMI) fish were correctly classified, and only 7% of the other fish were incorrectly classified to this group. There was much misclassification in the two central groups, and adjustment of the boundary between these two groups did not produce marked improvement (not shown).

Grouping into three categories by combining the two central groups resulted in substantial improvement in discrimination (83% correct) (Table 5). Shifting of the boundary between the northern and central group revealed that discrimination broke down when the southern

Table 1

Summary of parasites used for discrimination of stocks of adult Pacific halibut by locality. OR = Oregon–northern California, WA = SA1= southeast Alaska 1, SA2 = southeast Alaska 2, KP = Kenai Peninsula, KI = Kodiak Island, NI = Nagai Island, WAI = western bc = body cavity, o = organs, m = musculature, sw = stomach wall. Intensity = mean number of parasites per infected host.

			OR (*n*=23)		WA (*n*=14)	
Parasite	Site	Stage	%	Intensity	%	Intensity
Anisakis simplex	bc, o, m	larva	100	258.2 ±520.2	100	122.2 ±101.0
Corynosoma villosum	bc	juvenile	74	7.9 ±5.4	71	6.3 ±7.3
Corynosoma strumosum	bc	juvenile	52	5.6 ±6.4	50	6.3 ±5.2
Nybelinia surmenicola	sw	metacestode	17	2.8 ±2.9	14	4.0 ±4.2
Otodistomum sp.	sw	metacercaria	44	14.3 ±13.8	36	32 ±55.7
Pseudoterranova decipiens	bc, o, m	larva	44	2.5 ±2.1	21	2.3 ±1.5
Contracaecum sp.	bc	larva	0	0	0	0
Spirurid gen. sp.	sw	larva	22	1.4 ±0.5	50	11 ±24.7

	KP (*n*=21)		KI (*n*=26)		NI (*n*=13)	
Parasite	%	Intensity	%	Intensity	%	Intensity
Anisakis simplex	100	33.6 ±22.1	100	29.5 ±27.3	100	80.3 ±62.0
Corynosoma villosum	95	11.1 ±12.4	100	11.2 ±18.4	85	12.6 ±15.0
Corynosoma strumosum	19	1 ±0.0	27	1.3 ±0.5	8	2.0 ±0.0
Nybelinia surmenicola	43	4.2 ±3.9	65	29.5 ±106.6	39	42.2 ±89.0
Otodistomum sp.	14	2.0 ±1.7	4	1 ±0	8	1 ±0.0
Pseudoterranova decipiens	29	1.5 ±1.2	50	1.9 ±1.4	61	2.5 ±2.0
Contracaecum sp.	62	3.0 ±3.08	50	3.2 ±3.2	0	0
Spirurid gen. sp.	9	1.0 ±0	4	1 ±0.0	0	0

Table 2

Summary of parasites used for discrimination of stocks of juvenile Pacific halibut. NQC = northern Queen Charlotte Islands, NI = Nagai Island, UP = Unimak Pass, PI = Nunivak Island (central Bering Sea). bc = body cavity, o = organs, m = musculature, sw = stomach wall. Intensity = mean number of parasites per infected host.

			NQC (*n*=20)		KI (*n*=13)		NI (*n*=20)		UP (*n*=20)		PI (*n*=23)	
Parasite	Site	Stage	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity
Anisakis simplex	bc, o, m	larva	25	1.2	8	1.0 ±0	65	3.1 ±1.9	70	3.6 ±3.1	30	1.7 ±0.8
Corynosoma villosum	bc	juvenile	5	1 ±0.0	46	1.3 ±2.4	75	3.4 ±2.6	80	5.8 ±7.4	9	1.5 ±0.7
Corynosoma strumosum	bc	juvenile	0	0	8	1.0 ±0	0	0	5	1 ±0.0	48	1.2 ±0.4
Hysterothylacium aduncum	bc, o	juvenile	15	1 ±0.0	92	4.4 ±3.2	95	8.7 ±10.7	85	5.4 ±8.8	74	2.8 ±1.5
Nybelinia surmenicola	sw	metacestode	0	0	0	0	0	0	5	1 ±0.0	26	1.3 ±0.8
Pseudoterranova decipiens	bc, o, m	larva	0	0	8	1.0 ±0	25	1.4 ±0.9	15	1 ±0.0	4	6 ±0.0
Contracaecum sp.	bc	larva	0	0	15	1.0 ±0	10	5 ±5.7	0	0	0	0
Spirurid gen. sp.	sw	larva	0	0	0	0	5	2.0 ±0.0	0	0	0	0

Table 1

Washington, VI = southern Vancouver Island, SQC = southern Queen Charlotte Islands, NQC = northern Queen Charlotte Islands, Aleutian Islands, SB = southern Bering Sea, PI, Pribilof Island (central Bering Sea), SMI = St. Matthew Island (northern Bering Sea).

VI (*n*=32)		SQC (*n*=31)		NQC (*n*=8)		SA1 (*n*=20)		SA2 (*n*=29)	
%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity
100	381.4 ±357.1	100	167.8 ±101.4	100	76.1 ±47.6	100	81.8 ±141.1	100	44.0 ±57.0
94	8.8 ±7.4	94	13.7 ±24.3	100	5.9 ±7.4	90	10.9 ±16.6	93	16.1 ±32.0
44	3.6 ±5.2	39	1.8 ±1.5	25	2.0 ±0.9	15	1.7 ±0.6	52	1.9 ±1.0
19	16.0 ±31.9	3	1.0 ±0.0	50	13.3 ±23.8	30	11.8 ±25.1	52	4.1 ±2.0
9.4	18.3 ±30.0	39	8.3 ±13.9	38	4.7 ±2.3	35	13.0 ±11.0	21	8.3 ±11.0
16	1.2 ±0.4	13	1.5 ±0.6	25	2.0 ±0.0	25	3.2 ±4.4	69	3.1 ±3.0
3	1.0 ±0	0	0	50	3.8 ±4.9	40	3.5 ±2.2	45	2.0 ±2.0
3	1.0 ±0	0	0	0	0	15	2.3 ±1.2	10	2.8 ±2.0

UP (*n*=20)		WAI (*n*=20)		SB (*n*=29)		PI (*n*=14)		SMI (*n*=28)	
%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity
100	53.3 ±43.8	100	41.5 ±55.0	100	40.6 ±33.6	100	21.5 ±22.3	84	10.9 ±10.0
85	29.6 ±57.4	95	13.8 ±14.0	97	16.8 ±18.3	86	34.4 ±37.0	90	34.4 ±55.9
30	2.0 ±1.5	40	2.1 ±2.0	38	8.5 ±20.2	79	9.0 ±9.3	77	23.2 ±25.4
55	2.7 ±2.1	35	16.1 ±33.8	52	6.7 ±13.1	57	34.6 ±69.2	58	25.0 ±69.8
0	0	5	1 ±0	0	0	0	0	0	0
45	1.4 ±0.7	45	2.3 ±2.0	38	2.3 ±1.5	29	2.3 ±1.3	23	2.4 ±1.8
15	2.0 ±1.0	30	1.3 ±1.0	38	3.0 ±4.5	14	1.0 ±0	7	4.0 ±3.5
5	1.0 ±0.0	0	0	4	1 ±0.0	0	0	0	0

Bering Sea (SB) was included in the northern group (not shown). Inclusion of the northern Queen Charlotte Islands (NQC) in the southern group had little effect (81% correct classification) (not shown). These analyses indicated a southern (OR–SQC) group, a central (NQC–SB) group, and a northern (PI–SMI) group.

Classification into two categories (with SQC as the dividing line) provided no substantial improvement (87% correct) (not shown). Inclusion of NQC in the southern group had little effect (88% correct classification).

Discrimination of juveniles was poor with any organization of localities. The "best fit" classification correctly classified only 66% of the fish and there was substantial misclassification among the localities (Tables 6 and 7). Fish from the northern Queen Charlotte Islands (NQC) through Nagai Island (NI) separated reasonably well, but the majority of fish from the northernmost locality were also misclassified to this group. Note that parasite numbers and prevalences were low in the juveniles (Table 2).

Discussion

Our results show four things: 1) parasites clearly differentiate a group of southern adults; 2) parasites provide some evidence for a separation of the northernmost adults; 3) the differentiation is not always unequivocal; and 4) parasites do not differentiate groups of juvenile fish.

Skud (1977) concluded that southern and northern groups mixed extensively at all ages of their life history and that, although populations of adults may be largely discrete in the summer, any such discreteness was temporary because tagging evidence suggested more extensive winter migrations associated with spawning. Our data, on the other hand, suggest that there is some merit to the IPHC's early recognition of three stocks of adult halibut. Parasite data support the existence of two major groups of halibut and suggest the possibility of a third group in the central and northern Bering Sea. The high proportion of correct classifications based on parasites suggest that these differences are well established.

Recognition of three such groups is also supported by several of Skud's (1977) observations. He presented data suggesting that after fish home to spawning areas, southern and northern fish maintain reasonably separate migration circuits between feeding and spawning grounds. Data from Skud (1977) and more recent tagging data (Geernaert, 1996) also suggest that southern fish move less than their northern counterparts. Skud also recognized a resident population in the Bering Sea. These con-

Table 3

Cross validation results of a 15-category discriminant function classification of adult Pacific halibut in the northeast Pacific based on parasite data. Numbers of fish assigned to each locality and the corresponding percentage of the sample assigned to that category are shown. See Table 1 legend for key to abbreviations. Correct classifications are shown in bold (28% of 240).

True category	Assigned category														
	OR	WA	VI	SQC	NQC	SA1	SA2	KP	KI	NI	UP	WAL	SB	PI	SMI
OR	**4** **17%**	2 9%		1 4%	2 9%						2 9%		3 13%		
WA	2 25%	**2** **3%**			1 13%									1 13%	2 25%
VI		1 4%	**19** **73%**	2 8%	3 12%							1 4%			
SQC	1 4%	1 4%	10 40%	**11** **44%**							2 8%				
NQC					**2** **50%**	2 50%									
SA1		1 7%			1 7%	**4** **29%**		1 7%	1 7%	1 7%				3 21%	
SA2	1 4%				1 4%	2 9%	**1** **4%**	3 13%	3 13%	1 4%	1 4%		8 35%	1 4%	1 4%
KP						7 50%	1 7%	**1** **7%**	1 7%	1 7%	2 14%		1 7%		
KI						7 35%	2 10%	1 5%	**2** **10%**	1 5%	2 10%		3 15%	2 10%	
NI			1 14%		1 14%				2 29%	**1** **14%**	1 14%				
UP			2 14%			1 7%			2 14%	2 14%	**1** **7%**	2 14%	3 21%		1 7%
WAI						3 21%	1 7%	1 7%		2 14%	2 14%	**0**	5 36%		
SB		1 7%			1 7%	4 29%	3 21%	1 7%	2 14%	1 7%	2 14%	5 36%	**1** **7%**		2 14%
PI													1 13%	**3** **38%**	4 50%
SMI						1 5%			3 14%			3 14%		1 5%	**14** **64%**

clusions pose two questions. First, do fish from different groups mix extensively? Second, do such groups represent reproductive units or stocks?

Our analysis was based on a small set of larval parasites, all of which are known to be long-lived and do not multiply in the host. Other long-lived parasites such as the myxosporeans have been used in stock discrimination but were not included here because of a lack of abundance data. However, the decreased ability to detect differences because of the small data set was offset by an increased ability to detect the host's past activities. Most of these parasites live for at least several years; therefore, the presence and abundance of these parasites may indicate where the host has been over that time period. At least some of the individuals of each of the parasite species, however, were probably short-term acquisitions (lasting a few years); thus, there may be some bias in the data of the recent past.

Our data suggest less extensive movement of Pacific halibut in southern areas. Because parasites are generally more abundant in the south, southern fish may be more easily classified. Nevertheless, if the southern fish mingle extensively with more northern fish, there should be more similarity in the parasite faunas. In particular, central area fish should develop characteristics of southern fish. This did not happen, as is shown by the very low proportion of central fish misclassified as southern fish (Table 5). Our information cannot completely rule out the movement of southern fish to central areas during the spawning season, and then back to southern areas for the feeding season. Their long-lived parasite fauna, having been established in the distinct southern areas, would probably

Table 4

Cross validation results of a four-category discriminant function classification of adult Pacific halibut in the northeast Pacific based on parasite data. Numbers of fish assigned to a category and the corresponding percentage of the sample in that category are shown. Correct classifications are shown in bold (63% of 240). OR–SQC = Oregon–northern California to southern Queen Charlotte Islands, NQC–KP = northern Queen Charlotte Islands to Kenai Peninsula, KI–SB = Kodiak Island to southern Bering Sea, PI–SMI = Pribilof Islands to St. Matthew Island.

True category	Assigned category			
	OR–SQC	NQC–KP	KI–SB	PI–SMI
OR–SQC	**60** **79%**	3 4%	7 9%	6 8%
NQC–KP	3 5%	**28** **50%**	21 42%	4 7%
KI–SB	7 9%	23 30%	**41** **53%**	7 9%
PI–SMI		1 3%	6 20%	**23** **77%**

Table 5

Cross validation results of a three-category discriminant function classification for adult Pacific halibut in the northeast Pacific based on parasite data. Numbers of fish assigned to a category and the corresponding percentage of the sample in that category are shown. Correct classifications are shown in bold (83% of 240). OR–SQC = Oregon–northern California to southern Queen Charlotte Islands, NQC–SB = southeast Alaska to southern Bering Sea, PI–SMI = Pribilof Islands to St. Matthew Island.

True category	Assigned category		
	OR–SQC	NQC–SB	PI–SMI
OR–SQC	**63** **83%**	7 9%	6 8%
NQC–SB	10 7%	**112** **84%**	12 9%
PI–SMI		5 17%	**25** **83%**

Table 6

Cross validation results of five-category discriminant function classification for juvenile Pacific halibut in the northeast Pacific based on parasite data. Numbers of fish assigned to a category and the corresponding percentage of the sample in that category are shown. Correct classifications are shown in bold (44% of 62). NQC = northern Queen Charlotte Islands, NI = Nagai Island, UP = Unimak Pass, and PI = Nunivak Island (central Bering Sea).

True category	Assigned category				
	NQC	KI	NI	UP	PI
NQC	**9** **69%**	4 31%			
KI	1 14%	**5** **71%**	1 14%		
NGI	5 39%	3 23%	**3** **23%**	2 15%	
UP	5 39%		2 15%	**5** **39%**	1 8%
PI	6 38%	4 25%		1 6%	**5** **31%**

Table 7

Cross validation results of a three-category discriminant function classification for juvenile Pacific halibut in the northeast Pacific based on parasite data. Numbers of fish assigned to a category and the corresponding percentage of the sample in that category are shown. Correct classifications are shown in bold (66% of 62). NQC = northern Queen Charlotte Islands, NI = Nagai Island, UP = Unimak Pass, PI = Nunivak Island (central Bering Sea).

True category	Assigned category		
	NQC–NI	UP	PI
NQC–NI	**30** **91%**	3 9%	
UP	6 46%	**6** **46%**	1 8%
PI	10 63%	1 6%	**5** **31%**

not lose their southern character. Winter sampling could potentially determine if this is the case.

With respect to the Bering Sea, we suggest that the majority of the mixing occurs in the southern Bering Sea because classification breaks down when the southern Bering Sea is included in the northern region. This mixing is consistent with larval studies that show that larvae enter the Bering Sea through the Aleutian chain. Those fish may not disperse far into the Bering Sea. Rather, they either remain in the southern Bering Sea or migrate back to the Gulf of Alaska area (Skud [1977] believed that both occurred). A migration may explain why fish tagged in the Bering Sea tend to be recovered at greater distances from the tagging site than those tagged elsewhere (Geernaert, 1996). Migrations of the central and northern Bering Sea group appear to be in a more northerly direction (Skud, 1977), which would preclude mixing in the Aleutians and the Gulf of Alaska. Zoogeographic analysis with patterns of prevalence showed that Bering Sea parasites are rarely found outside the Bering Sea (Blaylock et al., 1998b).

The patterns identified in our analysis agree only in part with zoogeographic analyses (Blaylock et al., 1998b). The southern boundaries in both studies are in the vicinity of the Queen Charlotte Islands, providing additional support for the existence of a southern group of halibut. However, this analysis, unlike the zoogeographic analyses, indicated no sign of a division in the vicinity of Kodiak Island, suggesting that the division near Kodiak Island depends on short-lived species not included in this analysis. The evidence for the existence of a northern Bering Sea group is equivocal; it was supported by the clustering of localities by using prevalences and, to some degree, the clustering of individuals, but was not supported by any other analyses (Blaylock et al., 1998b).

With respect to juveniles, Skud's (1977) analysis clearly indicates compensatory movement from the Gulf of Alaska and southern Bering Sea to southern areas, and, as such, predicts that juveniles should have more similar parasite faunas among areas. Our data show this similarity, but there are significant caveats. First, our samples of juveniles came from areas that form a single group in the classification of adults. The sample from the northern Queen Charlottes is near the southern boundary of that group, and the sample from Nunivak Island is near the northern boundary. Samples of juveniles from other areas, particularly the southern area, should be examined to help clarify this issue. Second, and maybe more important, in these smaller fish, prevalences and intensities are low and perhaps hinder separation. However, because halibut at this stage are susceptible to bycatch in other fisheries (IPHC, 1996), management should probably consider juveniles a mixed stock to prevent impacts on future halibut populations in distant localities.

Overall, our analysis provides a less clear picture than that of Arthur and Albert (1993) for Greenland halibut in the northwest Atlantic. Part of the lack of clarity may be due to our use of the training and test set method rather than the bootstrapping method used by Arthur and Albert, which would increase the likelihood of correctly classifying similar fish. Also, Arthur and Albert were dealing with a very different system. Geological and oceanographic conditions around the Gulf of St. Lawrence are quite complex and create great potential for the isolation of stocks. The northeast Pacific is more open and has fewer isolating mechanisms than the northwest Atlantic. Further, the system is clinal (Blaylock et al., 1998b) and Pacific halibut are quite capable of migrating along the entire Pacific coast; therefore, less clear cut divisions are expected. Nevertheless, we successfully identified groups of fish, some with a high degree of accuracy.

Skud (1977) suggested that juveniles will, as adults, home to the areas in which they were spawned, making the existence of reproductive stocks at least possible. Modern molecular methods could address the issue. For example, molecular methods could potentially address the existence of separate stocks in the south and in the northern Bering Sea. The limited molecular studies done to date, however, have not elucidated any indentifiable stock structure because of limited sampling localities, the limited number of loci examined, and the use of juveniles only. Tsuyuki et al. (1969) examined a single serum hemoglobin transferrin locus in halibut from ten sites from Vancouver Island to the Bering Sea and found that only one southeast Alaska locality was different. Grant et al. (1984) found no differences between Gulf of Alaska and Bering Sea halibut at five loci but were able to distinguish northeast Pacific halibut from Japanese halibut. However, it is important to note that biochemical and genetic information measures differentiation at a different time scale than that reflected in parasite data (Lester et al., 1988). According to Grant (1984), movement of only a few Atlantic herring (*Clupea harengus*) may be sufficient to obscure true differences between different breeding stocks. Thus, even limited gene flow could obscure any differences in the loci examined.

Parasite or tagging information alone, however, can not determine whether or not the groups we identified are reproductive stocks. Therefore, all potential factors that might refine the halibut stock concept should be considered. The parasite data suggest a conservative approach to management that recognizes a mixed stock of juveniles and three potential stocks of adults—one in the south, another in the northern Bering Sea, and a third and largest centered in the Gulf of Alaska.

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Small-scale spatial and temporal variability in growth and mortality of fish larvae in the subtropical northcentral Gulf of Mexico: implications for assessing recruitment success

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Abstract—Extensive plankton collections were taken during seven September cruises (1990–93) along the inner continental shelf of the northcentral Gulf of Mexico (GOM). Despite the high productivity and availability of food during these cruises, significant small-scale spatial variability was found in larval growth rates for both Atlantic bumper (*Chloroscombrus chrysurus*, Carangidae) and vermilion snapper (*Rhomboplites aurorubens*, Lutjanidae). The observed variability in larval growth rates was not correlated with changes in water temperature or associated with conspicuous hydrographic features and suggested the existence of less-recognizable regions where conditions for growth vary. Cruise estimates of mortality coefficients (Z) for larval Atlantic bumper (n=32,241 larvae from six cruises) and vermilion snapper (n= 2581 larvae from four cruises) ranged from 0.20 to 0.37 and 0.19 to 0.29, respectively. Even in a subtropical climate like the GOM, where larval-stage durations may be as short as two weeks, observed variability in growth rates, particularly when combined with small changes in mortality rates, can cause order-of-magnitude differences in cumulative larval survival. To what extent the observed differences in growth rates at small spatial scales are fine-scale "noise" that ultimately is smoothed by larger-scale processes is not known. Future research is needed to further characterize the small-scale variability in growth rates of larvae, particularly with regard to microzooplankton patchiness and the temporal and spatial pattern of potential predators. Small-scale spatial variability in larval growth rates may in fact be the norm, and understanding the implications of this subtle mosaic may help us to better evaluate our ability to partition the causes of recruitment variability.

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For many marine fishes year-class strength undergoes large fluctuations because of the inherent variability in larval, postlarval, and juvenile survivorship (Hjort, 1914; Cushing, 1975; Lasker, 1975; Hunter, 1982; Houde, 1987; Goshorn and Epifanio, 1991; Pepin and Myers, 1991). Understanding and quantifying recruitment variability remains one of the greatest challenges in fisheries science today (Fritz et al., 1990; Cushing and Horwood, 1994; Leggett and Deblois, 1994; Mertz and Myers, 1995). Early survival rates are influenced not only by predation pressure but also by growth rate which can alter the duration of the larval stage when larvae are exposed to accumulative high mortality rates (Houde, 1987; Chambers and Leggett, 1987; Anderson, 1988; Bailey and Houde, 1989). Pepin (1991) formalized this concept by depicting the cumulative mortality (C) of a population from stage a to older stage b as the direct function of the instantaneous growth ($g[x]$) and mortality ($M[x]$) rates such that

$$C = \int_a^b \frac{M[x]}{g[x]} dx,$$

where x are factors that influence the vital rates (M and g) such as food availability, temperature, and abundance of potential predators.

Many questions remain concerning the causes of recruitment variability. Reasons for variability include the following: the inherent variability in growth and mortality rates and resulting survivorship; difficulties in estimating mortality rates with sufficient accuracy and precision; and the complex interrelationships among factors that affect survivorship of larvae (Parrish, 1973; Laurence, 1979; Houde, 1987; Beyer, 1989; Pepin, 1991). Houde (1989) hypothesized that cohort survivorship is more sensitive to small changes in vital rates in high latitude systems than in tropical or subtropical systems because the colder temperatures cause slower growth rates and longer larval stage durations, i.e. up to 100 days.

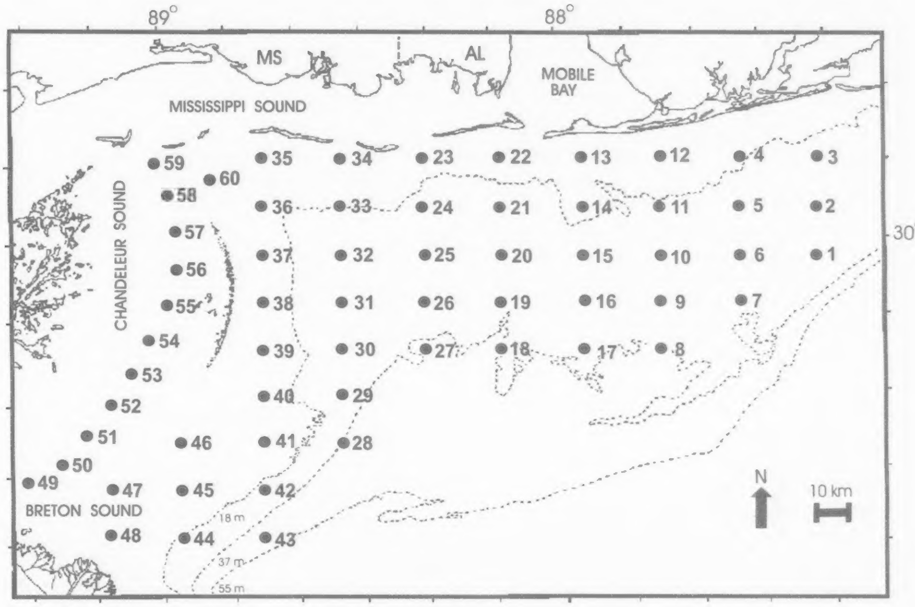

Figure 1

Station locations (•) of plankton collections in the northcentral Gulf of Mexico, September 1990 to 1993.

Pepin (1991) questioned this conclusion because he found no net effect of temperature on postlarval stage-specific mortality rates, although his study was based mainly on interspecific variation in mortality (Francis, 1994).

The objectives of our study were to determine if growth rates of Atlantic bumper (*Chloroscombrus chrysurus*, Carangidae) and vermilion snapper (*Rhomboplites aurorubens*, Lutjanidae) varied over small spatial scales in the northcentral Gulf of Mexico (GOM); determine the magnitude and variability of cruise estimates of larval mortality; and determine the potential influence of variability in these vital rates on cohort survivorship in a region where summer water temperatures approach 30°C and larval stage durations are as short as two to three weeks. Vermilion snapper is the most abundant species of snapper in the northern GOM (Goodyear and Schirripa[1]), and Atlantic bumper is the most abundant carangid.

Materials and methods

Sampling location and shipboard procedures

Seven, three-day cruises were conducted in inner-shelf waters of east Louisiana, Mississippi, and Alabama during September 1990–93 (Fig. 1). Cruise estimates of larval mortality were determined by using data from all cruises during the four-year period. Specimens used for age and growth analyses were collected during 14–16 September 1991 when larvae of both vermilion snapper and Atlantic bumper were abundant.

Larvae were collected with a 1 m × 1.4 m Tucker trawl fitted with a 333-µm mesh nitex net and a mechanical flowmeter. Oblique tows were taken from the surface to within a few meters of the bottom and back to the surface at a speed of approximately two knots (1.0 m/s). Samples were concentrated and stored in 95% ethanol. At each sampling location surface, midwater and bottom measurements of temperature and salinity were obtained with water-bottle casts.

Laboratory procedures

Lengths of larvae were measured to the nearest 0.1 mm by using a stereomicroscope (12× or 25×) fitted with an ocular micrometer and the larvae were sorted into 0.5-mm size classes. Measurements were taken from the tip of the snout to the end of the notochord in preflexion larvae (notochord length), and from the tip of the snout to the end of the urostyle or hypural plate (whichever was more distal) in flexion or postflexion larvae (standard length). Larval shrinkage was not accounted for because between-station and between-cruise comparisons of growth rates were made with larvae that were preserved in the same concentration of ethanol and stored for approximately the same length of time. Shrinkage of ethanol-preserved larvae is not large, e.g. 0 to 7% (Theilacker, 1980; Fowler and Smith, 1983; Kruse and Dalley, 1990). It is unlikely that size-related shrinkage effects would have biased our estimates of growth rate because these estimates were based on larvae in similar size classes. Additionally, Theilacker (1980) found that preserving northern anchovy larvae after they had died during net capture caused additional shrinkage, but this shrinkage was at a constant rate that was proportional to fish length. Catches of larvae were standardized to account for sampling effort and expressed as number of larvae under 10 m^2 of sea surface. This method of expressing the abundance of larvae more accurately reflects station differences in abundance than a mean density (number/m^3) when fish larvae are not homogeneously distributed throughout the water column, as has been shown with other species from this area (Lyczkowski-Shultz and Steen, 1991), and when sampling (station) depths are variable, as they were in our study.

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[1] Goodyear, C. P., and M. J. Schirripa. 1991. A biological profile for vermilion snapper with a description of the fishery in the Gulf of Mexico. Unpublished report CRD 87/88-16, 53 p. Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami FL 33149.

Dry weights of larvae were determined by rinsing specimens with distilled water, drying for 24 h at 60°C, and weighing to the nearest 0.1 µg. Both sagittal otoliths were removed following rehydration for 12 h. Otoliths were mounted convex side up on a glass microscope slide with a drop of Pro-Texx mounting medium and a cover slip. Otolith growth increments were counted in the sagittal plane under oil immersion (1250×).

A total of 140 Atlantic bumper larvae and 119 vermilion snapper larvae were selected for age analyses. Specimens were selected from stations where a wide size range of larvae were collected. Daily otolith increment formation has been validated for larval Atlantic bumper (Leffler and Shaw, 1992). Daily increment formation has not been validated for vermilion snapper; however, otolith increments observed in larval vermilion snapper were very similar in width and spacing to validated daily increments found in red snapper from this region (Szedlmayer, 1998; Lyczkowski-Shultz and Comyns[2]). Slopes of age-length regressions for larval vermilion snapper (n=11) and red snapper (n=25) collected during July 1992 in our study area were not significantly different, further indicating that vermilion snapper, like red snapper, form daily otolith growth increments.

Otolith growth increments were counted by using the sagitta (right or left) that provided the most distinct incremental zones. Paired t-test analyses showed no significant difference ($P \leq 0.05$) in diameters of left and right sagittae in both vermilion snapper (n=11) and Atlantic bumper (n=20). Daily increments were counted along the longest axis of the otolith from the core to the outer edge. Otoliths were read once by a single reader, and a random subsample of otoliths from vermilion snapper (n=30) and Atlantic bumper (n=30) was read a second time to examine within-reader variability. Otolith increment counts differed by one day for only two of the 30 otoliths during the second reading for both species.

Data analysis

Age-length and age-weight relationships were described by using the exponential equation

$$L \text{ or } W = \exp(a + bt),$$

where, in its linearized form,
L = notochord or standard length in mm;
W = dry weight in mg;
a = Y-intercept;
b = slope of regression line (instantaneous growth rate); and
t = age of larvae in days.

Values of a and b were calculated from the linearized form of the growth equation after the length or weight data were transformed to their natural logarithms. The instantaneous growth rate (b), i.e. the slope of the log-transformed, age-length or age-weight relationship, is also referred to as the growth coefficient. Caution must be exercised when making dry-weight comparisons because of preservation-induced weight loss. Kristoffersen and Salvanes (1998) found that body weight loss was as high as 37–39% in small ethanol-preserved mesopelagic fishes. Dry weight data were used only to determine whether relative changes in weight tracked trends found in age-length relationships. Analysis of covariance (ANCOVA) was used to determine if differences existed among station estimates of instantaneous growth coefficients (Sokal and Rohlf, 1969; SigmaStat, 1995). If differences were found (α=0.05), the simultaneous test procedure (STP; Sokal and Rohlf, 1969) was used as an *a posteriori* test to determine station differences.

Cruise estimates of total larval abundance for each size class (catch curves) were developed for Atlantic bumper and vermilion snapper by summing the abundance estimates of each size class under 10 m^2 of sea surface from each station. Length-frequency distributions were converted to age-frequency distributions by assigning ages to mid-points of the 0.5-mm size classes with the age-length relationship previously described. Age-class abundances were corrected for stage duration by dividing the abundance estimate of each age class by their respective durations (Houde, 1977). It is necessary to correct for stage durations of age classes if growth rates are nonlinear. Stage durations of age classes were determined by assigning ages based on previously determined growth equations to end-points of the 0.5 mm size classes. This customary method for constructing catch curves relies on the rarely examined assumption that larvae at different sampling locations are growing at similar rates. The high r^2 values of the age-length relationships (0.92 for Atlantic bumper; 0.84 for vermilion snapper) that resulted when aged larvae from all stations were combined indicated that growth rates over the study area were similar enough to justify use of this technique.

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[2] Lyczkowski-Shultz, J., and B. H. Comyns. 1992. Early life history of snappers in coastal and shelf waters of the north-central Gulf of Mexico late summer/fall months, 1983–1989, 12 p. + 9 tables, 17 figures. Technical Report submitted to the National Marine Fisheries Service, Southeast Regional Office, 9721 Executive Center Drive North, St. Petersberg, FL. 33702.

Cruise estimates of larval mortality rates for Atlantic bumper and vermilion snapper larvae were estimated from catch curve analyses (e.g. Houde, 1977; Essig and Cole, 1986; Watanabe and Lo, 1988; Deegan, 1990; Comyns et al., 1991). The instantaneous mortality rate (Z) was estimated by the slope of the exponential function relating duration-corrected larval abundance and age (Ricker, 1975):

$$D_t = D_0 \exp(-Zt),$$

where D_t = total abundance of larvae at time t;
D_0 = total abundance of individuals at time 0;
Z = instantaneous mortality rate; and
t = age of size class in days since spawning.

Age and abundance of size classes were fitted to this exponential function with a nonlinear least squares routine, and only the descending limb of the regression was used to estimate mortality rates. To reduce potential biases associated with 1) any trend of increasing variance in the length-at-age distribution with increasing age, and 2) net avoidance by larger larvae, only Atlantic bumper and vermilion snapper larvae smaller than 6.1 mm and 6.0 mm, respectively, were used to estimate mortality rates. Kolmogorov-Smirnov two-sample tests showed no significant differences ($P<0.05$) between size-frequency distributions for day versus night catches within this size range for vermilion snapper and Atlantic bumper larvae.

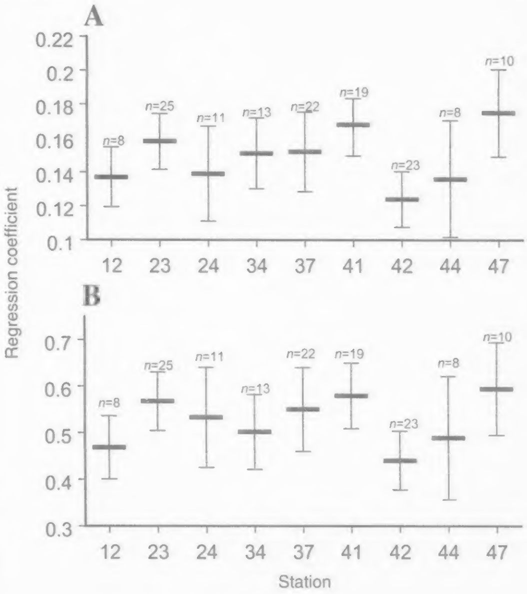

Figure 2

Growth coefficients (horizontal bars) for Atlantic bumper larvae collected at nine stations in the northcentral Gulf of Mexico, during 14–16 September 1991. Vertical lines represent 95% confidence intervals around the growth coefficients, and numbers above bars depict sample sizes; (**A**) shows age versus ln length growth coefficients and (**B**) shows age versus ln dry-weight growth coefficients.

Results

Age and growth

Atlantic bumper larvae, which were commonly found throughout the study area, ranged from 2 to 14 days old, 1.4 mm to 8.1 mm in length, and 0.003 mg to 1.446 mg in dry weight. Estimates of age versus length growth coefficients were not similar for all stations (ANCOVA; $P=0.001$). The STP revealed no overlap in 95% confidence intervals around growth coefficients for larvae collected at station 42 and larvae collected at stations 41, 23, and 47 (Figs. 2A and 3). According to their respective growth equations, Atlantic bumper larvae at station 42 grew at approximately 0.43 mm/d and reached a length of 6 mm in approximately 13.3 days. Larvae collected at adjacent station 41 grew faster, approximately 0.63 mm/d, and reached a length of 6 mm in 10.4 days.

Similarly significant differences in station estimates ($n=9$) of age–dry-weight growth coefficients were also found (ANCOVA; $P=0.01$), and growth coefficients for larvae collected at station 42 were significantly different from larvae collected at stations 41 and 23 (STP; Fig. 2B). By 11 days, the estimated dry weight of an Atlantic bumper larva at station 42 was 0.38 mg, whereas at station 41 larvae gained weight faster and the estimated dry weight of an 11-d-old larva was 0.58 mg. Adjacent stations 41 and 42 were 10 km apart, and water temperatures at these two locations were very similar. Surface temperatures varied by only 0.1°C (28.7°–28.8°C), and surface and midwater temperatures varied by only 0.5°C. Daily surface water temperatures recorded at a weather bouy within the study area showed that temperatures varied by less than 2°C during the 31-d period prior to our study.

Significant differences in station ($n=7$) growth rates of vermilion snapper larvae were also found in our 14–16 September 1991 cruise (ANCOVA; $P=0.03$). Vermilion snapper larvae ranged from 4 to 16 days old, 2.5 mm to 6.5 mm in length, and 0.014 mg to 0.696 mg in dry weight. Growth coefficients for larvae collected at stations 15 and 25 were significantly different (STP; Figs. 4A and 5). According to their respective growth equations, vermilion snapper larvae collected at station 15 reached a length of 5 mm in 10.7 days, whereas larvae collected at station 25 grew more slowly and did not reach a length of 5 mm until 12.6 days. Stations 15 and 25 were located 17 km apart on the inner shelf at water depths of 29–30 m. Surface water temperatures at these stations varied by 2.2°C, and both surface and midwater station temperatures differed by less than 2°C.

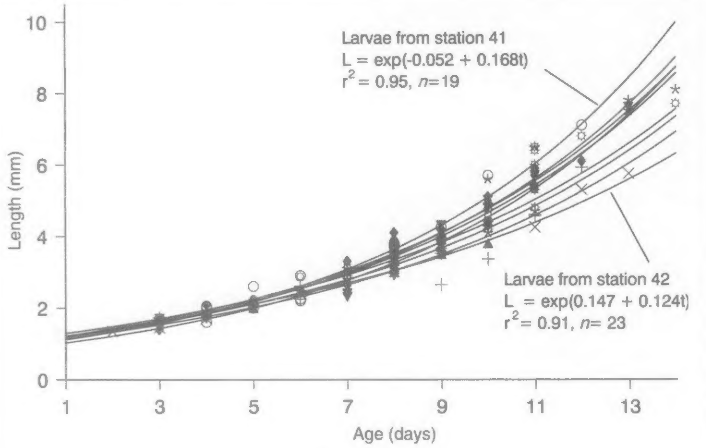

Figure 3

Age versus length data for Atlantic bumper larvae (n=140) collected at nine stations in the northcentral Gulf of Mexico during 14–16 September 1991. Highlighted are the age-length relationships at two adjacent stations where growth rates differed. L = notochord or standard length in mm; t = larval age in days.

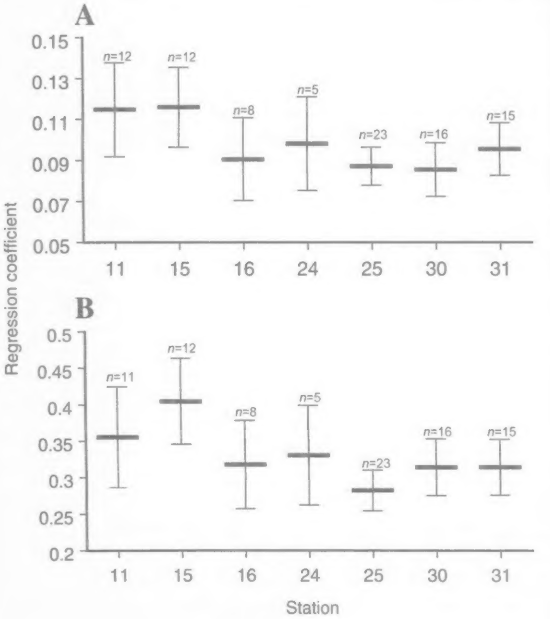

Figure 4

Growth coefficients (horizontal bars) for vermilion snapper larvae collected at seven stations in the northcentral Gulf of Mexico during 14–16 September 1991. Vertical lines represent 95% confidence intervals around the growth coefficients, and numbers above bars depict sample sizes. (**A**) shows age versus ln length growth coefficients, and (**B**) shows age versus ln dry-weight growth coefficients.

Differences in age versus dry-weight growth coefficients were also significantly different (ANCOVA; P=0.03) and once again stations 15 and 25 (Fig. 4B) were significantly different (STP). Vermilion snapper larvae gained weight faster at station 15 where an 11.0-d-old larva had an estimated dry weight of 0.28 mg. At station 25 the estimated dry weight of this same larva was only 0.17 mg. Although vermilion snapper larvae were collected at most of the stations within the study area (Fig. 1), abundances were low at shallow (12–14 m depth) stations immediately south of the Mississippi–Alabama coast, and larvae were never collected at stations within Chandeleur Sound. These stations were very shallow (4–9 m).

Although our study did not assess microzooplankton prey availability, macrozooplankton dry-weight estimates varied widely over space and time. At the 33 stations east of Chandeleur Sound where larvae of vermilion snapper and Atlantic bumper used in our study were captured, macrozooplankton dry-weight estimates at 20 stations exceeded 3g/100 m^3, and at eight of those stations values exceeded 5g/100 m^3. Seven days later only at five of the 33 stations were macrozooplankton dry-weight estimates >3g/100 m^3 and at no station did estimates exceed 5g/100 m^3.

Mortality estimates

Atlantic bumper was generally the most abundant species in plankton collections; 32,241 larvae were collected during six cruises conducted in September of 1990, 1991, and 1993. Mortality rates were not estimated for Atlantic bumper larvae collected during the two cruises conducted in September 1992 because abundances of larvae were very low. When station abundance data were pooled for each of the six cruises, size-frequency distributions gener-

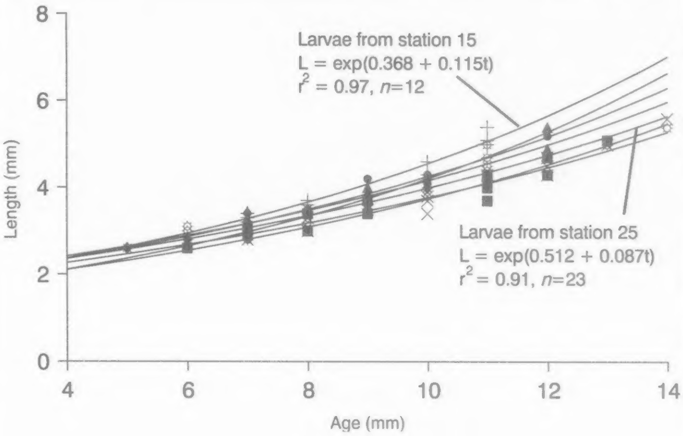

Figure 5

Age-length data for vermilion snapper larvae (n=89) collected at seven stations in the northcentral Gulf of Mexico during 14–15 September 1991. L = body length in mm; t = larval age in days. Highlighted are the age-length relationships at two stations where growth rates differed.

ally exhibited a similar decrease in abundance with successively larger size classes; however, the smallest size class (1.1–1.6 mm) was the most abundant in only three of the six cruises (Fig. 6, A, B, and F). This under representation of the smallest size class in several cruises was likely influenced by several potential factors, including a possible decrease in spawning prior to sampling and patchiness of eggs and newly hatched larvae caused by the aggregation of spawning adults. Cruise-estimates of mortality coefficients, which were derived by pooling data from all stations sampled during a cruise and omitting the smallest size class, ranged from 0.20 to 0.37 (Fig. 6). It is likely that mortality rates varied between stations, but as previously mentioned, an average cruise-estimate of mortality was determined to ascertain a realistic level about which the effects of small variations in growth rates could be assessed on the cumulative survival of larvae. Standard errors of Z estimates were low, ranging from 0.02 to 0.05.

Size-frequency distributions were derived for vermilion snapper larvae (n=2581) taken during two September 1991 cruises, and single late-September cruises in 1992 and 1993 (Fig. 7) when vermilion snapper larvae were abundant. Mortality estimates could not be estimated for five September cruises during the period 1990–93 because relatively few larvae were collected. Larvae collected during three of the four cruises when they were abundant showed a steady decrease in abundance of successively larger size classes (Fig. 7, A, C, and D). During the fourth cruise (late September 1991; Fig. 7B), the size-frequency distribution showed a distinct peak in abundance of intermediate-size larvae (4.0-mm size class). Mortality coefficients (Z) from the four cruises ranged from 0.19 to 0.30 and standard errors for the mortality coefficients were relatively low ranging from 0.02 to 0.05.

Discussion

Plankton collections taken in the northcentral GOM during September showed that growth and mortality rates did vary in time and space for Atlantic bumper and vermilion snapper larvae, and that these differences were great enough to significantly impact the cumulative survival of larvae in a subtropical climate where larval-stage durations are short (i.e. two weeks). Growth and mortality estimates of vermilion snapper larvae were previously unknown. Two previous studies of growth and mortality of Atlantic bumper larvae (Leffler and Shaw, 1992; Sánchez-Ramírez and Flores-Coto, 1998) provided no information on variability in growth rates at small spatial scales and no estimates of mortality during the period when our study was conducted.

Highly significant between-station differences in growth rates were observed for both Atlantic bumper and vermilion snapper larvae. The largest difference in age versus length growth coefficients for Atlantic bumper larvae was found at adjacent, inner-shelf stations located approximately 10 km apart. According to growth equations, the faster growing larvae grew to a length of 6 mm 2.9 days sooner than larvae at the adjacent station, and differences in larval weight gain as expressed by dry weight of 11-d-old larvae varied by over 30%. Water temperatures at these two stations were extremely similar; surface temperatures varied by only 0.1°C, midwater temperatures varied by 0.4°C, and surface and midwater temperatures varied by 0.5°C. It is likely that a similarly small temperature differential was present during the two-week period prior to this cruise, i.e. throughout the life of larvae used in our study because daily surface water temperatures recorded at a weather bouy within the study area during the previous month showed

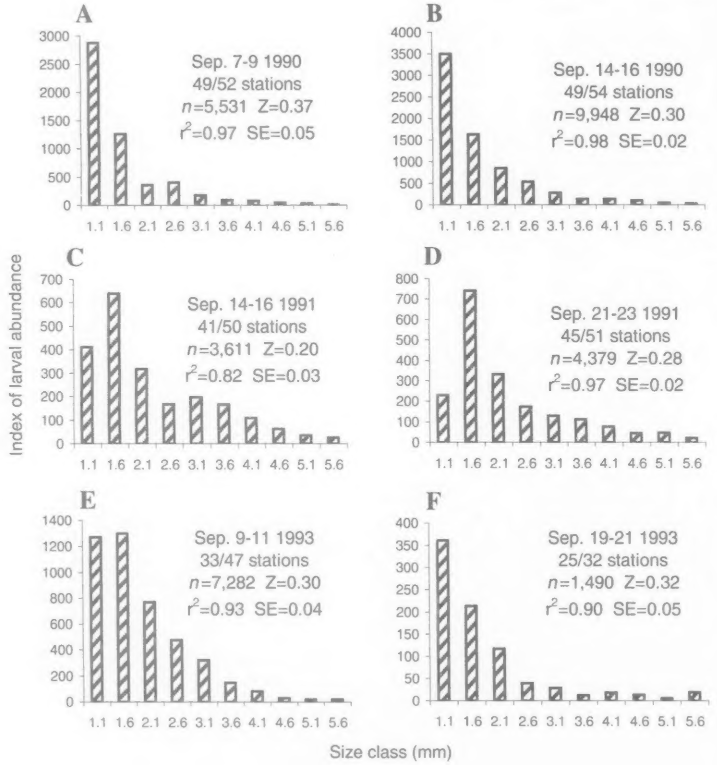

Figure 6

Size-frequency distributions of Atlantic bumper larvae collected during six cruises in the northcentral Gulf of Mexico during September 1990, 1991, and 1993. Values of Z, SE, and r^2 refer to mortality curves produced from the duration-corrected, age-frequency distributions (omitting the smallest size class). The fraction listed for each cruise refers to positive (larvae were collected) stations/total stations sampled. Abundance of each size class is pooled estimates of station abundances.

that temperatures varied by less than 2°C. Significant differences in both age versus length and age versus weight relationships were also found for vermilion snapper larvae collected at relatively close stations (i.e. 17 km apart). Water temperatures at these two stations were similar but differed by as much as 2°C. Faster growing larvae reached a length of 5 mm approximately 2 days sooner than larvae growing in nearby areas. Significant differences were also found in larval weight-gain; dry weight of 11-d-old larvae from different stations varyied by as much as 65%.

The variability in growth rates that we observed was likely caused by station differences in food availability and size-selective mortality, and to a lesser degree by water temperature. Unfortunately our data did not allow us to determine the individual effects of these factors on observed growth rates. At least for Atlantic bumper, the effects of temperature changes were probably minimal.

Larval survival is generally more influenced by factors other than temperature. Morse (1989) found a positive correlation between length-dependent mortality and surface water temperature for 26 larval fish taxa and attributed this to increased predator consumption rates (caused by increased metabolic rates) at higher temperatures. He also concluded that increased growth due to increases in temperature alone would generally impart no advantage to reduce larval mortality because of the concomitant increased predatory consumption rates. Increased larval-stage duration at cooler temperatures is not necessarily associated with increased cumulative larval mortality because predation rates decline with decreasing temperature (Pepin, 1991; Francis, 1994). Methot (1981) concluded that after correcting for the effect of temperature on growth rates, the mean growth rate of larval fish is an indicator of the degree to which larval growth, and presumably survival, is food limited.

We acknowledge that size-selective predation, i.e. "culling out" the slowest (or fastest) growing larvae, could have produced the differences in size-at-age structure among

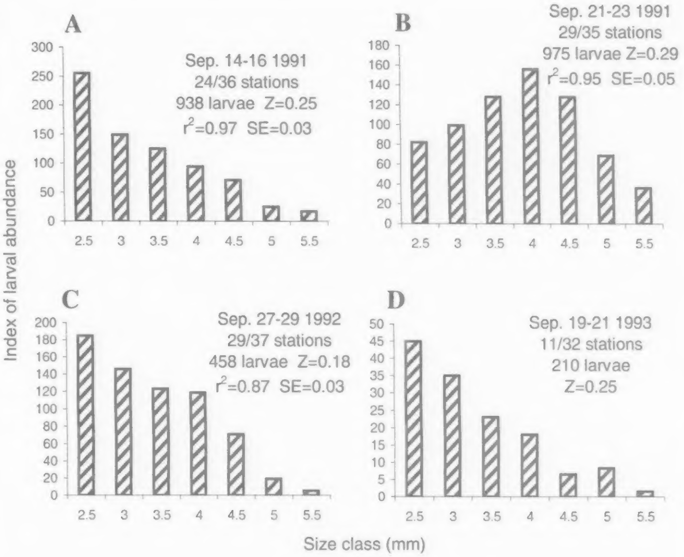

Figure 7

Size-frequency distributions of vermilion snapper larvae collected during four cruises conducted in the northcentral Gulf of Mexico during September 1991, 1992, and 1993. Estimates of *Z*, SE, and r^2 refer to mortality curves produced from duration-corrected age-frequency distributions. The fraction listed for each cruise refers to positive (larvae were collected) stations/total stations sampled. Abundance of each size class was pooled from estimates of station abundances.

stations that we observed. However, predation pressure seems unlikely to have been the primary cause of this variability. If among-station variability in size-selective mortality was largely responsible for the differences in larval growth rates, one would expect the variability in size-at-age at each station to be quite variable and this was not the case. Stations where the effects of size-selective mortality were minimal (or less) should have had both fast and slow growing larvae present; yet coefficients of determination (r^2) were ≥0.90 for age versus length regressions at all stations. Furthermore, there was no correlation between observed growth rates and r^2 values which would be expected if size selective predation was largely responsible for the variability in growth rates that we observed.

Many studies have shown that food availability has a large influence on growth rates of larvae (e.g. Houde and Schekter, 1981; Buckley et al., 1987; Pepin, 1991) and it is likely that station differences in food availability influenced our observed differences in larval growth rates. We did not collect the small size-fraction of prey eaten by fish larvae, but our data did reveal extensive spatial and temporal variability in the abundance of macrozooplankton. Macrozooplankton biomass at station 42, where relatively slow growth of Atlantic bumper occurred, was 2.6 mg/100 m^3 whereas at station 41, where larvae were growing faster, macrozooplankton dry weight (3.9 g/100 m^3) was 50% higher. When all stations were considered, there was no correlation between macrozooplankton dry weight and growth coefficients of larvae, but macrozooplankton biomass was certainly very patchily distributed. For most stations there was at least a 50% difference in macrozooplankton dry weight between one of the adjacent stations. It is equally likely that the smaller size fraction of zooplankton that fish larvae eat were also very patchily distributed. In addition, several other studies have shown that primary production in the northern GOM is dynamic and spatially heterogenous (Lohrenz et al., 1990, 1994; Redalje et al., 1994), although these studies have focused on regions influenced by discharge from the Mississippi and Atchafalaya rivers.

In many studies the significant spatial variability in growth rates of field-caught larvae cannot be explained by changes in water temperature. These reported differences in growth rates have often been associated with factors such as storm events (Lasker, 1975; Maillet and Checkley, 1991), different geographical locations (Mokness, 1992; Nixon and Jones, 1997; Allman and Grimes, 1998;), or distinct hydrographic features such as tidal fronts (Munk, 1993) and riverine discharge plumes (Govoni et al., 1985; DeVries et al., 1990; Lang et al., 1994). All studies in the GOM that have reported spatial differences in larval growth rates have involved comparisons in the vicinity of the Mississippi River discharge plume (Govoni et al., 1985; DeVries et al., 1990; Lang et al., 1994; Allman and Grimes, 1998). The observed variability in larval Atlantic bumper and vermilion snapper growth rates reported in our study was not associated with conspicuous hydrographic features (e.g. hydrographic convergence zones) and suggests the existence of less-recognizable regions where conditions for growth vary.

Cruise estimates of mortality were determined to ascertain a realistic level about which the effects of small variations in growth rates on the cumulative survival of larvae could be assessed. In order to do this, data from all stations sampled during a cruise were pooled. This provided the most reliable general estimate of mortality for each cruise despite likely site-specific differences in mortality rates that are extremely difficult to measure. Such pooling of data is not unusual; in fact Morse (1989) suggested that samples should be summed over the larval production cycle. Essig and Cole (1986) estimated mortality rates of larval alewives (*Alosa pseudoharengus*) by using both converted length-frequency distributions, as we did, and actual age-frequency distributions. They found no statistical difference between the two methods. Pepin and Miller (1993), however, warned that because variability in observed length-at-age increases with larval age (Chambers et al., 1988), analyses that use size in older fish to represent age may yield biased estimates of mortality rates. Yet, Pepin and Miller (1993) observed that their mortality rates, which were estimated by using size as a proxy for age, were consistent with mortality rates reported from other environments and species. Ideally, all fish would be aged, but for our study this was not possible because of the large sample sizes, multiple cruises, and the labor-intensive nature of otolith preparation for age determination.

Atlantic bumper larvae were extremely abundant (n= 32,241 for six cruises), and cruise estimates of age-frequency distributions showed consistent, well-defined descending limbs. Estimates of mortality coefficients (Z) for Atlantic bumper larvae were similar for September cruises conducted in the same year. For example, in 1990 the two cruise estimates of Z were 0.37 and 0.30, in 1991 the two Z estimates were 0.20 and 0.28, and in 1993 estimates of Z were 0.30 and 0.32. These mortality rates are similar to estimates reported by Leffler and Shaw (1992) during four September cruises in the same area during 1986–87 (Z=0.17–0.35) and by Sánchez-Ramírez and Flores-Coto (1998) in the southern Gulf (0.15–0.30). In addition, standard errors of the mortality estimates from our study were low, ranging from 0.02 to 0.05.

Cruise estimates of mortality rates for vermilion snapper were determined during four cruises when larvae were relatively abundant (n=2581). The descending limbs of three of the size-frequency distributions uniformly spanned all seven size classes, but during one cruise the middle size class was most abundant and the descending limb of this size-frequency distribution was restricted to four size classes. However, mortality rates were quite similar during all cruises (Z=0.19 to 0.30) and each had a low standard error (SE=0.02 to 0.05).

Collections of Atlantic bumper and vermilion snapper larvae were taken when water temperatures ranged from 25° to 30°C, and the mortality coefficients estimated from these collections were similar to those reported for other species under similar temperature regimes. Houde (1989) summarized vital rates of six species of larval fish as reported in seven studies where the mid-points of water temperatures at the time of collection ranged from 26° to 28°C. Most of these studies generated a range of mortality estimates, and the mid-points of the ranges reported in six of these studies varied from 0.21 to 0.38, values that are consistent with the mortality estimates (0.19 to 0.39) that we observed.

Our primary reason for estimating mortality rates was to ascertain a realistic level about which small variations could be assessed for potential effects on the cumulative survival of larvae, particularly in conjunction with variability in larval growth rates. Our method assumes a constant birth rate, or recruitment rate into the population, and assumes that fish leave the population only through death. There is clearly some expected variability in the degree to which these assumptions were met; however, based on the similarity of mortality estimates, not only between cruises but also to previously published estimates, it is concluded that our mortality estimates are biologically meaningful.

The well-accepted fisheries paradigm holds that changes in year-class strength are determined by variability in mortality during early life stages (Sissenwine, 1984; Houde, 1987; Bailey and Houde, 1989; Cushing and Horwood, 1994). Despite extensive efforts to understand the causes of recruitment variability, significant questions remain because the operant factors are likely to be interrelated parts of the ecosystem dynamics that comprise a multidimensional system (Ellersten et al., 1995). For example, it is not the mortality or growth rate alone that determines survival during the early life-stages, but the ratio M/G, the stage-specific mortality rate (Pepin, 1991). Examining previously published information, Houde (1989) found an exponential increase in predicted larval-stage duration with decreasing water temperature for 26 species of larval fishes and surmised that when temperature is low, small changes in growth rates can induce large changes in larval-stage duration that may significantly affect the recruitment process.

To determine the potential effects that variability in vital rates might have on the cumulative survival of larvae, hypothetical numbers of newly hatched Atlantic bumper were projected to a size of 6 mm under the influence of the growth and mortality rates we observed in the study area (Table 1). According to these vital rates, and a hypothetical initial cohort size of 1×10^6 individuals, 124,930 larvae survive to a length of 6 mm under the scenario of relatively fast growth and low mortality (G=0.61 mm/d; Z=0.20). If the growth rate is slowed (G=0.45 mm/d) and it takes approximately three days longer to reach a length of 6 mm, the number of larvae that survive to this length is reduced by 44%. If the slower growing larvae are exposed to the higher mortality rate (Z=0.37), cumulative survival of larvae decreases by an order of magnitude, and only

Table 1

Hypothetical survival of Atlantic bumper larvae to a size of 6 mm under the influence of growth and mortality rates observed in the study area.

Initial number in cohort	Instantaneous mortality coefficient (per day)	Age of 6-mm larva (d)	Number of 6-mm larvae
1×10^6	0.20	10.4	124,930
1×10^6	0.20	13.3	69,948
1×10^6	0.30	10.4	44,157
1×10^6	0.30	13.3	18,499
1×10^6	0.37	10.4	21,322
1×10^6	0.37	13.3	7292

7292 larvae survive to a length of 6 mm. Houde (1987) published a projection on the mortality of larvae exposed to hypothetical levels of mortality and growth rates, but the theoretical exercise used relatively long larval-stage durations (45–56 days). Results of our study show that even in a subtropical climate where larval stage durations may be as short as two weeks, relatively small changes in observed larval growth rates, particularly when combined with small differences in mortality, can have a large impact on cumulative larval survival. To what extent the observed differences in growth rates at small spatial scales are fine-scale "noise" that is ultimately smoothed by larger-scale processes is not known. Future research is needed to further characterize the small-scale variability in growth rates of larvae, particularly with regard to microzooplankton patchiness and the temporal and spatial pattern of potential predators. Small-scale spatial variability in larval growth rates may in fact be the norm, and understanding the implications of this subtle mosaic may help us to better evaluate our ability to partition the causes of recruitment variability.

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Temporal changes in population density, fecundity, and egg size of the Hawaiian spiny lobster (*Panulirus marginatus*) at Necker Bank, Northwestern Hawaiian Islands

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Abstract—Fecundity (F, number of brooded eggs) and egg size were estimated for Hawaiian spiny lobster (*Panulirus marginatus*) at Necker Bank, Northwestern Hawaiian Islands (NWHI), in June 1999, and compared with previous (1978–81, 1991) estimates. Fecundity in 1999 was best described by the power equations $F = 7.995\ CL^{2.4017}$, where CL is carapace length in mm (r^2=0.900), and $F = 5.174\ TW^{2.758}$, where TW is tail width in mm (r^2=0.889) (both n=40; P< 0.001). Based on a log-linear model ANCOVA, size-specific fecundity in 1999 was 18% greater than in 1991, which in turn was 16% greater than during 1978–81. The additional increase in size-specific fecundity observed in 1999 is interpreted as evidence for further compensatory response to decreased lobster densities and increased per capita food resources that have resulted either from natural cyclic declines in productivity, high levels of harvest by the commercial lobster trap fishery, or both. The density decline is well-documented by a fivefold decrease in commercial catch-per-trap-haul (CPUE) during the late 1980s to early 1990s and by a similar decrease in research CPUE for all-sized (including juvenile) *P. marginatus* through the 1990s. Fecundity increases are consistent with decreases in median body size at sexual maturity, first described from comparisons of 1977–81 and 1986–87 specimens and consistently observed thereafter during the 1990s. Egg size covaried with fecundity; in 1999, individual eggs within broods had a 11% greater mass (15% greater volume) than eggs brooded in 1991. Implications of these observations are discussed in relation to possible future management measures for a commercial lobster fishery in the NWHI. More generally, our findings argue for the need to routinely reevaluate compensatory responses in exploited stocks of lobsters and other resources.

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The endemic Hawaiian spiny lobster (*Panulirus marginatus*) has been the principal target of the Northwestern Hawaiian Island (NWHI) commercial trap fishery since the mid- to late 1970s (Uchida and Tagami, 1984; Polovina, 2000). Landings and exvessel (wholesale) value have fluctuated greatly over the years, in part because of annual variations in trapping effort and a 1-yr fishery closure in 1993, but have been generally lower during the 1990s because of declines in oceanic productivity and recruitment and increased exploitation (Polovina and Moffitt, 1995; Polovina et al., 1995). The fishery was closed in 2000 because of increasing uncertainty in the population models used to assess stock status. In December 2000 President Clinton, through Executive Order (EO) 13178 and later through EO 13196, established the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve which may prohibit commercial lobster fishing in the NWHI for at least 10 years. Annual research surveys of the National Marine Fisheries Service (NMFS), Honolulu Laboratory, have demonstrated a decline (Fig. 1) in spiny lobster density (CPUE, catch-per-trap-haul) at Necker Bank, NWHI, one of the sites at which spiny lobsters have been consistently targeted since about the mid-1970s.

Polovina (1989) first described a density-dependent decrease in median body size at sexual maturity and an increase in asymptotic body size for spiny lobster at Necker Bank, based on a contrast between specimens collected during 1977–81 and 1986–87. DeMartini et al. (1993) observed an increase in size-specific fecundity for specimens collected in 1991, used to further characterize the Necker Bank population's status after-exploitation. Compensatory increases in juvenile growth and survival and increases in size at maturity as responses to decreased density following increased fishery exploitation have been observed for other spiny lobster stocks (e.g. see Pollock, 1995a, 1995b).

In this article, our objectives were to estimate recent (1999) berried female fecundity and egg size for the Hawaiian spiny lobster at Necker Bank and to relate these to prior, analogous estimates for lobsters collected in 1991 and 1978–81, analyzed by DeMartini et al. (1993). We then use the 1999 fecundity estimates and 1999 commercial catch data to characterize recent egg production by the Necker Bank population. We conclude with a brief discussion of the management implications of compensatory reproductive responses by the population.

Methods and materials

All specimens used in this study were trapped from Necker Bank surrounding Necker Island (23°34′N, 164°42′W), NWHI, during the species' mid-spring to mid-summer peak period of egg brooding at mid-archipelago latitudes (Uchida and Tagami, 1984). Specimens for 1999 were collected on a cruise of the NOAA ship *Townsend Cromwell*. Details of specimen collection and processing of the 1978–81 and 1991 samples are described by DeMartini et al. (1993). The 1999 samples were collected during 9–22 June 1999 from the bank terrace at a median 27-m depth by using molded plastic ("Fathom Plus") traps baited with 1 kg of mackerel (*Scomber japonicus*) and fished with a standard (overnight) soak.

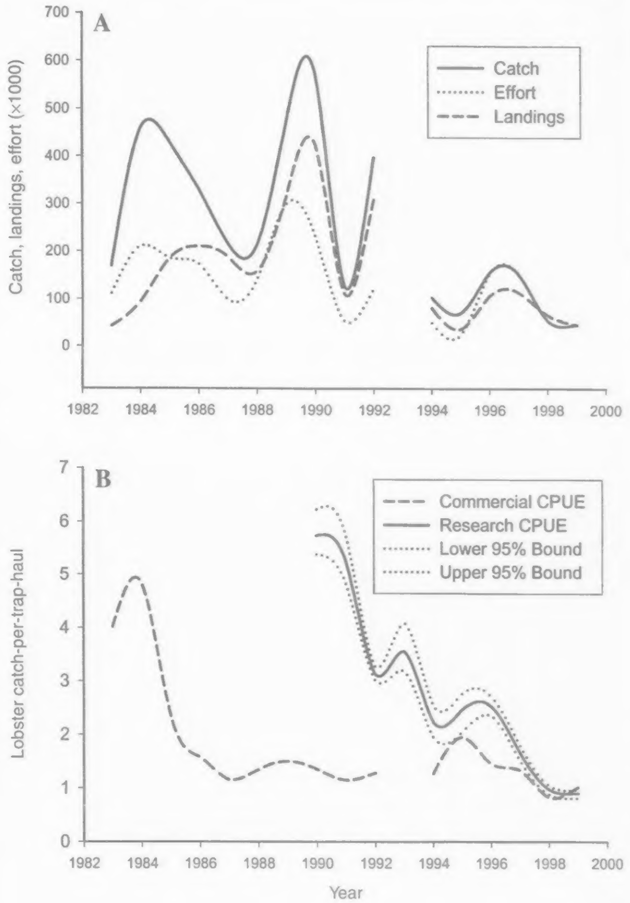

Figure 1

Time series plots of (**A**) the Northwestern Hawaiian Islands (NWHI) commercial trap catch and landings of *Panulirus marginatus* (no. of lobsters × 1000) and effort (no. of trap-hauls × 1000); and (**B**) total *P. marginatus* catch-per-trap-haul (CPUE) at Necker Bank, NWHI, during the 1983–99 commercial fishing seasons and as assessed on 1988–1999 lobster research cruises. (Research CPUE data are lacking for years prior to 1988.) Dashed lines framing the research CPUE curve in **B** represent bootstrapped 95% confidence intervals (DiNardo et al.[2]).

Shipboard processing

Specimens were processed identically to those collected in June 1991. All specimens were processed alive within minutes of trap retrieval. Both carapace length (CL: defined as the straight line distance between the anterior edge of the supraorbital ridge and the posterior edge of the carapace along the dorsal midline) and tail width (TW: defined as the straight line distance across the abdomen at the widest spot between the first and second abdominal segments) of each specimen were measured to 0.1 mm with dial calipers. TW is the present metric of choice for lobster management in the NWHI trap fishery. CL was the metric used to characterize body size in many prior research and management studies of the species, and its measurement was needed for comparison with results of studies made prior to the mid-1980s. Berried (ovigerous) females were scored for egg developmental stage by using a gross visual proxy (brooded eggs noted as either orange or brown in color to the unaided eye). Berried specimens were individually flash-frozen for laboratory evaluation ashore.

Laboratory analyses

Fecundity, here defined in the limited sense of a single brooded egg mass (see Chubb, 2000), was estimated for 5–10 females per 5-mm TW class in order to provide at least 40 total specimens spanning the entire size range for analyses. Except for sample sizes, procedures were identical to those used for the 1991 collection. Only females bearing orange egg clusters with embryos lacking visible melanin pigment (early embryonic development) were considered in order to minimize the probability of physical damage, egg loss, and fecundity underestimation during capture and handling, which is an apparent problem only for broods of heavily pigmented (brown), late-development eggs with soft capsules (DeMartini, unpubl. data). Frozen specimens were thawed overnight at 3°C. All four pairs of egg-bearing pleopods were then removed from the abdomen, gently blotted (damp-dry) on a paper towel, and weighed individually to 0.1 mg on an electric microbalance. Eggs were then carefully teased off pleopod setae with jeweler's forceps and stored after being wrapped in cool, damp paper towels to minimize evaporative weight loss. Individual pleopods were then reweighed and the weight of each pleopod's egg complement was calculated by difference. Three subsamples of 0.1–0.2 g, each comprising about 700–1000 eggs total (about 100 eggs per pleopod, pooled over all 8 pleopods), were next weighed to 0.1 mg, their component eggs counted, and relative fecundity (RF, number of eggs per gram of brooded eggs) was calculated as a simple ratio, with the three subsamples used to calculate a mean and standard error of RF. Fecundity (*F*, defined

Table 1

(**A**) Summary catch statistics (*Townsend Cromwell* research cruise, Necker Bank, June 1999) and (**B–D**) fundamental linear-mass interrelationships for body and egg sizes of female Hawaiian spiny lobster (*Panulirus marginatus*) at Necker Bank, Northwestern Hawaiian Islands.

A Female catch statistics	Total		Berried		$TW_{\text{all females}}$		TW_{berried}	
	n	%	*n*	%	median	range	median	range
	834	54.6	350	42.0	50.1	24–72	51.1	38–72

B Relation of tail width to carapace length and vice versa; model: $Y = aX + b$

$TW = 0.6087\ CL + 4.44$ and $CL = 1.5772\ TW - 4.00$, [$r^2=0.963$, $n=825$, $P<0.001$]

where TW = tail width in mm, CL = carapace length in mm, and *a* and *b* are fitted constants.

C Relation of body weight to carapace length; model: $Y = aX^b$

$BW = 0.00090\ CL^{\ 2.9952}$, [range: 51.9–114.7 mm CL, $n= 197$, $P<0.001$]

where BW = total body weight in g, and CL = carapace length in mm, for unberried females (source: Uchida and Tagami [1984]).

D Relation of egg weight to egg diameter; model: $Y = aX^b$

$EW = 0.3985\ ED^{2.2472}$, [$r^2=0.833$, $n=40$, $P<0.001$]

where EW = egg weight in 0.001 mg, and ED =egg diameter in mm.

as the total number of pleopod-brooded eggs) was calculated as the product of mean RF and total weight of the brooded egg mass. Pilot tests indicated that this procedure estimated *F* with coefficients of variation (CV, SD/mean × 100%) consistently <5%. Subsamples of 25 eggs were randomly taken from each female's total egg complement and the diameter of individual eggs were measured (random axis) at 500× magnification by using a dissecting microscope and an optical micrometer. Average individual egg weight was also independently derived as the ratio of the weight to numbers of eggs present in the parent sample.

Statistical analyses

Relations of female body size to fecundity and body size to egg size were evaluated for the 1999 samples by using both linear and nonlinear least squares procedures (proc REG, proc NLIN) of PC SAS for Windows v. 6.12 (SAS Institute, 1990a, 1990b). Analysis of covariance (ANCOVA; proc GLM; SAS Institute, 1990c; Chubb, 2000) was used to compare size-specific fecundity estimates of Necker Bank *P. marginatus* among the three exploitation periods: 1978–81, 1991, and 1999. Subseasonal variation within spawning seasons was controlled by the aforementioned restriction on month of specimen collection, and single collections were assumed to provide accurate characterizations within exploitation periods. Fecundity data used to characterize the 1978–81 and 1991 periods at Necker Bank are listed in Appendix A of DeMartini et al. (1993). Analogous comparisons of size-specific egg sizes were limited to the 1991 and 1999 periods because no data on variance of egg sizes were available for the 1978–81 samples (DeMartini et al., 1993). Body-size–fecundity relations were allometric, hence log-linear (see Somers, 1991); natural logarithms were used for ANCOVAs and regressions of log-linear relations.

An index of reproductive potential (IRP; Kanciruk and Herrnkind, 1976) was computed for the 1999 specimens in order to determine the size classes of females that contributed most to population egg production. The IRP was constructed by using data for female *P. marginatus* caught by the commercial fishery at Necker Bank during 1999, collected by several contracted fishery observers.

Results

Fecundity and egg size of lobsters in 1999

Fecundity A number of the female *Panulirus marginatus* trapped on the research cruise at Necker Bank during June 1999 were berried (Table 1). The estimated fecundity of 40 females, spanning 54.3 to 105.4 mm CL (39.3–67.4 mm TW, see CL-TW relation; Table 1), ranged more than fivefold, from 109,865 to 590,530 eggs (Appendix A). Fecundity was positively and nonlinearly related to TW (Fig. 2) and CL and best described by the power equations $F = a\ TW^b$ and $F = a\ CL^b$, respectively, as

$$F = 5.1743\ TW^{\ 2.7580}, \quad [r^2=0.889]$$

and

$$F = 7.9952\ CL^{2.4017}$$

[$r^2=0.900$, both $n=40$, $P<0.001$.]

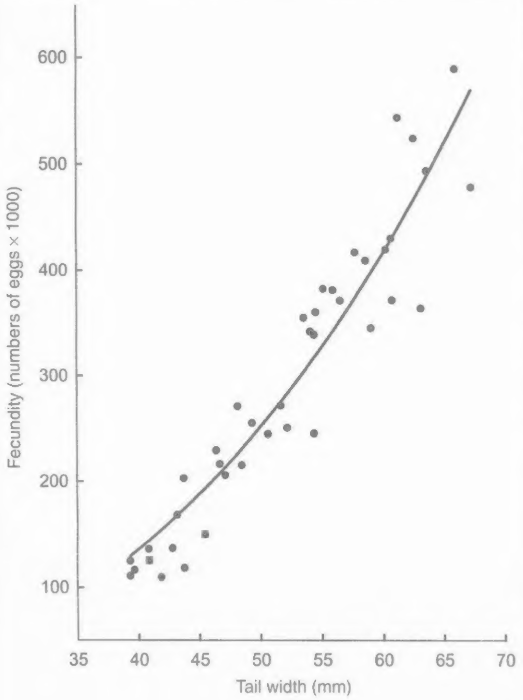

Figure 2

Scatterplot and fitted power curve describing the relation between fecundity (no. of brooded eggs×1000) and tail width (TW, in mm) for *Panulirus marginatus* collected at Necker Bank, 1999.

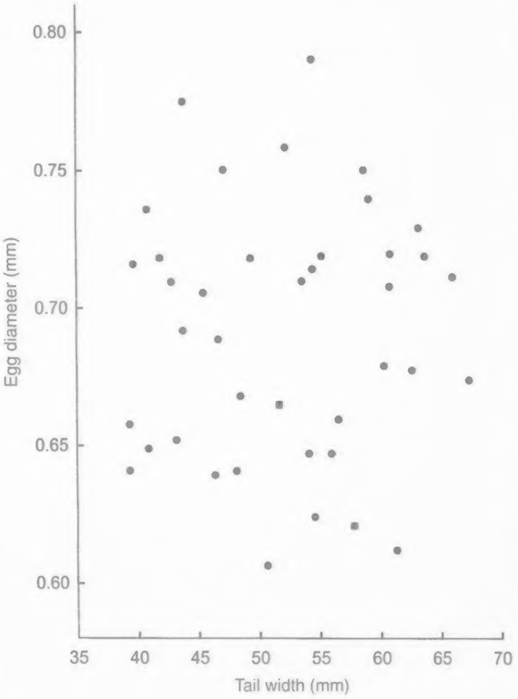

Figure 3

Scatterplot describing the relation between egg diameter (mm) and tail width (TW, in mm) for *Panulirus marginatus* collected at Necker Bank, 1999.

The standard errors of b were 0.1787 and 0.1472, respectively. A log-linear fit of the F-CL data ($\mathrm{Ln}F=2.5533\ \mathrm{Ln}CL+1.3977$) was nominally inferior ($r^2=0.886$) to the curvilinear fit but was required for the general linear model used in the ANCOVA comparisons that follow below. Fecundity subsamples averaged 1.5 ±0.14(SE)% of total brooded egg mass weight. Brooded egg masses weighed an average 51.4 g and ranged from 15.8 to 109.2 g. CVs of the three replicate estimates of RF averaged 1.2 ±0.11%. Mean RF was 5882 ±160(SE) eggs per g of brooded eggs and ranged nearly twofold from 4030 to 7930 eggs per g of eggs among the 40 females. Based on the aforedescribed nonlinear best fit, the fecundity of the median-size (53.8 mm TW, 80.9 mm CL) female caught at Necker Bank in 1999 by the commercial trap fishery was an estimated 306,400 ±90,200 (95% CI) eggs.

Egg size The mean (±SE) diameter of early-stage eggs carried by the 40 berried females was 0.69 ±0.007 mm, with a range of 0.61 to 0.79 mm. Analogous median (25th, 75th percentile) diameters were 0.70 (0.65, 0.72) mm. The corresponding egg weights were 0.17 ±0.005 and 0.18 (0.15, 0.20) mg (range: 0.13–0.25 mg). Individual egg size (diameter: Fig. 3; weight) was unrelated (both $P>0.63$) to female body size (TW). Individual egg weight was a power function of egg diameter (Table 1).

Temporal comparisons of fecundity and egg size

Fecundity Size-specific fecundities differed among the three periods, and body-size–adjusted means differed for each period (Table 2, Fig. 4). Size-adjusted mean fecundity in 1999 was 18% greater than in 1991, which in turn was 16% greater than during 1978–81. Lobster in 1999 thus exhibited a cumulative 36% increase in size-specific fecundity over that described for lobster collected during 1978–81. The statistical power (1 minus β, where β is the probability of making a type-II error) to detect an effect size equal in magnitude to the changes observed between 1978–81, 1991, and 1999 was estimated as >97% at $\alpha=0.05$.

Egg size Brooded eggs on average were about 5% greater in diameter (equivalent to 15% greater volume assuming the volume of a sphere, $V=4/3\ \pi r^3$) and were 11% heavier in 1999 compared to 1991 (Table 3). The precision of our

Table 2

(**A**) ANCOVA and (**B**) component least squares regression statistics for log-linear ($LnY = lna + bLnX$) relations of fecundity (F) to carapace length (CL) for *P. marginatus* caught at Necker Bank during three periods: 1978–81, 1991, and 1999. Natural logs are used throughout. Underlines illustrate that the least-square means for each period differ from one another. MSE = mean square error.

A ANCOVA model: $LnF = LnCL + \text{period}$ (r^2=0.855; root MSE=0.1843)

Factor	df	MS	*F*	*P*
Model	3	6.82	199.6	0.0001
Ln*CL*	1	17.16	502.1	0.0001
Period	2	0.87	25.5	0.0001
Ln*CL* × period (P=0.27—ns; not included in final model)				
Error	105	0.03		
Total	108			

$\underline{12.426} > \underline{12.284} > \underline{12.119}$

$\underline{1999} > \underline{1991} > \underline{1978\text{–}81}$

B Regression models: $LnY = Lna + bLnX$

1978–81	$LnF = 2.7994 + 2.1569\ LnCL$, r^2=0.708, n=35, P<0.001, SE a=1.0367, SE b=0.2412
1991	$LnF = 1.5859 + 2.4778\ LnCL$, r^2=0.881, n=34, P<0.001, SE a=0.6934, SE b=0.1607
1999	$LnF = 1.3977 + 2.5533\ LnCL$, r^2=0.886, n=40, P<0.001, SE a=0.6452, SE b=0.1485

measurements was sufficient for the observed change in egg diameter to have had an 87% chance of being detected at $\alpha = 0.05$.

Individual and population egg production

Based on the IRP of Kanciruk and Herrnkind (1976), most egg production by the Necker Bank population of *P. marginatus* in 1999 was by small adults (<60 mm TW) that now dominate the population (Table 4). Large adults (>60 mm TW), although highly fecund, are now too rare to contribute substantially to total population egg production (Table 4).

Table 3

(**A**) ANCOVA and (**B**) component least squares regression statistics for linear relations of egg diameter (ED, in eyepiece units, × 0.020=mm) to carapace length (CL, mm) of *P. marginatus* caught on research cruises to Necker Bank during 1991 and 1999. See Table 2 caption for additional details.

A ANCOVA model: $ED = CL + \text{period}$ (r^2=0.142; root MSE=2.193)

Factor	df	MS	*F*	*P*
Model	2	27.36	5.69	0.005
CL	1	3.33	0.69	0.41
Period	1	46.85	9.74	0.003
CL × period (P = 0.81—ns; not included in final model)				
Error	69	4.81		
Total	71			

$\underline{0.691} > \underline{0.658}$

$\underline{1999} > \underline{1991}$

B Regression models: $ED = a + b\ CL$

1991	$ED = 31.1646 + 0.0230$ CL, r^2=0.021, n=32, P<0.001, SE a=2.1224, SE b=0.0282
1999	$ED = 33.5760 + 0.0128$ CL, r^2=0.006, n=40, P<0.001, SE a=2.1768, SE b=0.0274

Discussion

Size-specific fecundity and egg size

Fecundity The initial 16% increase in body size-specific fecundity between 1978–81 and 1991 occurred while commercial CPUE decreased fivefold. Unlike commercial data, research CPUE data were collected at fixed stations (including juvenile habitat), were uninfluenced by increased catchability (the targeting of larger adult lobster in more productive habitats by commercial fishermen), and continued to show a decline of similar magnitude during the 1991–99 period when size-specific fecundity increased an additional 18% (Fig. 1B). Thus both observed fecundity responses occurred simultaneously with declining lobster densities. The cumulative 36% increase in size-specific fecundity observed for Necker Bank *P. marginatus* over a >20-yr period of exploitation is not unreasonable given the evidence for concurrent, compensatory declines in body size at sexual maturity in this population (Polovina, 1989; DeMartini et al.[1]). Density-dependent changes in somatic growth, survival rates, and body sizes at sexual maturity have been described for numerous other palinurid species (Pollock, 1995a, 1995b). At least one case study provides further evidence for reproductive compensation. Chittleborough (1979) documented a decreased interval between broods as a response to increased exploitation in the Western Australian rock lobster, *P. cygnus*. Prior to the present study, the study of DeMartini et al. (1993) was the only published record of changes in size-specific fecundity in a spiny lobster, perhaps attributable to density declines resulting from exploitation, although perhaps only reflecting natural interannual variation independent of fishing (Pollock, 1995b).

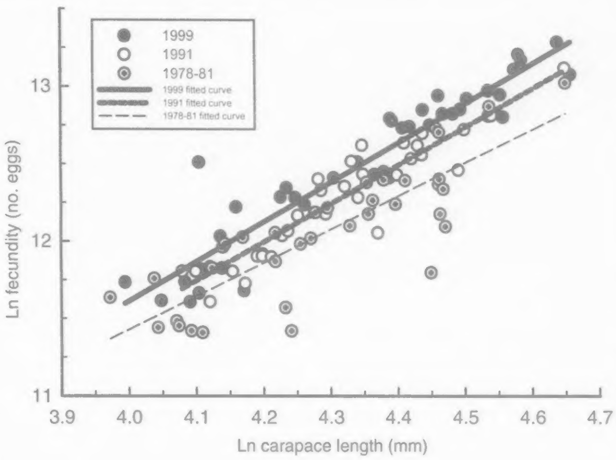

Figure 4

Log-linear scatterplot of fecundity (ln no. of brooded eggs) versus carapace length (ln CL, in mm) for *Panulirus marginatus* collected at Necker Bank during three periods (1978–81, 1991, and 1999).

The fecundity update for 1999 in this article further supports DeMartini et al.'s (1993) original interpretation of an increase in size-specific fecundity as a density-dependent response at lower population densities. Other data on body size at sexual maturity for the period 1988–99, to be reported elsewhere (DeMartini et al.[1]), extend the temporal pattern of smaller body size at sexual maturity first documented during 1986–87, after 10 years of exploitation, by Polovina (1989). The observed decrease in size at maturity could have been caused by slower growth (Pollock, 1995a) resulting from lower levels of oceanic productivity (Polovina et al., 1994, 1995). However, if smaller size at maturity has been a proximal response to decreased rather than increased per capita food availability, it is inconsistent with the simultaneous increases in size-specific fecundity and egg size which have occurred. Evidence for changes in the nutritional status of *P. marginatus* at Necker Bank during 1991–95 is equivocal (Parrish and Martinelli-Liedtke, 1999). Resolution of whether the lower densities of spiny lobsters at Necker Bank have resulted from natural declines in productivity, increased fishery exploitation (or both) would require comparative evaluations for lobsters collected from fished as well as unfished control areas at the bank; unfortunately, as of 1999 unfished lobster habitat at Necker Bank does not exist.

The observed increase in size-specific reproductive output of *P. marginatus* probably has been a phenotypic response to lower densities and higher per capita food availabilities at Necker Bank. It is unlikely, given the 3-yr generation time of *P. marginatus* (Uchida and Tagami, 1984) and relatively short (20+ yr) period over which the responses have occurred, that a genetic, rather than phenotypic, dynamic has been involved. More extensive comparisons of the egg productions of *P. marginatus* populations among Necker and other NWHI banks differing in natural and fishery-induced densities would be necessary to further distinguish natural variation from fishing effects. Complete resolution of this issue would require quantitative comparisons of growth rates and ages at maturity for a lengthy series of year classes of *P. marginatus* at Necker Bank and elsewhere.

Egg size Our data demonstrate that egg size can vary substantially among same-size *P. marginatus* collected during the midpoint of a single breeding season, as does fecundity among same-size females. It should not be surprising, then, that average population egg size has covaried with fecundity, even if egg size is body-size independent. The observed change in mean egg size between 1991 and 1999 could not have been due to either developmental or subseasonal changes because we evaluated egg size by consistent methods, using only early-development broods collected during the month of June. It is possible, although unlikely, that the larger eggs (hence larvae) produced in 1999 were somehow of inferior quality and had lower hatching success and poorer subsequent survival.

Intraspecific variation in egg size has rarely been described in spiny lobsters (Pollock, 1995a, 1997). Annala (1991) suggested that egg size increases with body size for a cold-temperate species, *Jasus edwardsii*, from mainland New Zealand. Egg size is unrelated to female body size in tropical *Panulirus argus* (Fonseca-Larios and Briones-Fourzan, 1998). In one particularly detailed study of the egg size dynamics of a small-bodied Caribbean palinurid, *P. guttatus*, Briones-Fourzan and Contreras-Ortiz (1999) detected no relation of egg size to female body size, even though egg size varied nearly twofold among females ranging over twofold in carapace length.

Few studies have documented temporal changes in egg size for palinurid lobsters. A seasonal decline in egg size

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[1] DeMartini, E. E., R. B. Moffitt, and P. Kleiber. 2002. Unpubl. data. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.

Table 4

Index of reproductive potential (IRP) calculated for female *Panulirus marginatus* caught by the Northwestern Hawaiian Islands commercial trap fishery at Necker Bank in 1999. IRP = $(A \times B \times C)/D$, where A= proportion of total females in each 1-mm TW class (×100%), B = proportion of berried females per 1-mm class (×100%), C = estimated brood size of the median-size female in each class ($\times 10^3$ eggs), and D = a constant (0.015788) used to standardize the most productive size class to 100% (Kanciruk and Herrnkind, 1976). E = % of total egg production; $F = E/A$, a class-specific measure of egg productivity.

TW class (mm)	Total no. of females	No. of berried females	*A*	*B*	*C*	IRP	*E* ($\times 10^3$)	*F* ($\times 10^3$)
<39	27	1	0.42	0.43	114	0.00	0.03	35.17
39–40	20	4	0.32	0.17	131	0.05	0.13	40.59
40–41	28	5	0.45	0.21	140	0.09	0.20	43.48
41–42	32	4	0.51	0.17	150	0.08	0.24	46.51
42–43	41	8	0.66	0.34	160	0.23	0.33	49.67
43–44	52	10	0.84	0.43	171	0.39	0.44	52.96
44–45	74	20	1.19	0.85	182	1.17	0.67	56.38
45–46	117	30	1.88	1.28	193	2.95	1.13	59.95
46–47	152	40	2.44	1.71	205	5.43	1.55	63.65
47–48	233	81	3.74	3.46	218	17.88	2.53	67.50
48–49	301	100	4.83	4.27	231	30.20	3.46	71.49
49–50	358	132	5.75	5.64	244	50.15	4.35	75.63
50–51	453	178	7.28	7.61	258	90.43	5.82	79.92
51–52	442	176	7.10	7.52	272	92.09	5.99	84.36
52–53	441	171	7.08	7.31	287	94.13	6.30	88.96
53–54	425	170	6.83	7.26	302	95.00	6.40	93.71
54–55	363	147	5.83	6.28	318	73.84	5.75	98.62
55–56	395	174	6.34	7.44	335	100.0	6.58	103.7
56–57	367	159	5.89	6.79	352	89.19	6.42	108.9
57–58	297	117	4.77	5.00	369	55.74	5.45	114.3
58–59	313	119	5.03	5.08	387	62.66	6.03	119.9
59–60	250	88	4.02	3.76	405	38.78	5.04	125.6
60–61	227	99	3.65	4.23	425	41.48	4.80	131.5
61–62	194	84	3.12	3.59	444	31.47	4.29	137.6
62–63	142	57	2.28	2.44	464	16.34	3.28	143.9
63–64	119	37	1.91	1.58	485	9.29	2.87	150.3
64–65	105	36	1.69	1.54	507	8.32	2.65	156.9
65–66	64	27	1.03	1.15	529	3.97	1.68	163.7
66–67	53	18	0.85	0.77	551	2.29	1.45	170.7
67–68	43	18	0.69	0.77	574	1.93	1.23	177.9
68–69	33	14	0.53	0.60	598	1.20	0.98	185.3
69–70	26	6	0.42	0.26	622	0.42	0.80	192.8
70–71	16	5	0.26	0.21	647	0.23	0.52	200.6
71–72	7	2	0.11	0.09	673	0.04	0.23	208.5
72–73	9	1	0.14	0.04	699	0.03	0.31	216.7
>73	7	2	0.11	0.09	782	0.01	0.08	242.3
Total	6226	2340	100.00	100.00		100.00		

for all-sized females has been observed in two Caribbean species, *Panulirus inflatus* (Gracia, 1985) and *P. argus* (Fonseca-Larios and Briones-Fourzan, 1998). Briones-Fourzan and Contreras-Ortiz (1999), however, could detect no difference in egg size among *P. guttatus* sampled during three consecutive years. Mean egg size declined within the spawning season, but this decline reflected a loss in mass caused by embryonic development within individual eggs rather than the production of smaller eggs later in the breeding season (Briones-Fourzan and Contreras-Ortiz, 1999). Pollock (1995c) noted that *P. guttatus* produces unusually few, but large eggs for a shallow-water tropical palinurid.

Using the CL-to-body-weight regression listed in Table 1, we estimated an inverse index of egg size (Pollock, 1997) for Necker Bank *P. marginatus* in 1999 that was 660 eggs per g total body weight. Such small eggs are typical within the derived lineage of shallow-water, subtropical and tropical members of the genus (Pollock, 1997).

We could find no other studies documenting changes in egg size as a response to density fluctuation in palinurid lobsters. Prior to the mid-1990s, information on temporal and size-related patterns of fecundity and egg size were largely restricted to cold- and warm-temperate members of the genus *Jasus* and *Panulirus* (Pollock, 1995c, 1997). Perhaps egg size, like size-specific fecundity, is phenotypically labile in tropical reef species of the genus *Panulirus* for which high and variable predation pressure makes such plastic responses adaptive. More research on size-specific, individual reproductive output is needed for *P. marginatus* and other tropical reef species of spiny lobsters.

It is unknown whether egg size lability in *P. marginatus* has a genetic or environmental basis. One could perhaps evaluate this for individual females by repetitively measuring egg subsamples from successively brooded egg masses of berried tagged and recaptured females. Fixed but differing egg sizes among individual females would be consistent with a genetic basis. On the other hand, changes in the size of eggs produced by the same individual female in successive broods would suggest that environmental factors are involved.

Management implications

One of our observations has major relevance to the management of *P. marginatus* in the NWHI lobster fishery. Based on the IRP of Kanciruk and Herrnkind (1976), egg production by the Necker Bank population of *P. marginatus* was dominated by the 50–57 mm TW classes in 1999, which together contributed >43% to population egg production (Table 4). Even though each large (>60 mm TW) individual produces a disproportionately great number of eggs, large females are now so poorly represented in the population that they no longer drive population egg production (Table 4). The eggs produced by smaller (50–57 mm TW) females are more important to the population now than before exploitation. In 1996 a "retain all" size policy was established for the commercial fishery, replacing a 50-mm-TW minimum size limit used previously, in part because of the high mortality of discarded lobsters (DiNardo et al., 2002). If a commercial lobster fishery with a minimum size limit were to be reinstated in the NWHI, a minimum size larger than the previous (50 mm TW) should be considered. Our findings on the size distribution of population egg production indicate that smaller adult females, which now produce most of the population's eggs, should be further protected, perhaps by using larger escape vents in traps. Doing so would increase total population egg production and might assist in countering recruitment overfishing (Botsford, 1991; Pollock, 1993). *Panulirus marginatus* production at Necker Bank historically and presently dominates archipelago-wide production by the species; this production is supported by empirical catch data (DiNardo et al.[2]) as well as modeling of its recruitment dynamics (Polovina et al., 1999). Augmenting egg production by the Necker Bank population might significantly bolster stock-wide productivity. The body size distribution of egg production by *P. marginatus* at other NWHI banks is presently unknown, however, and egg production by large females elsewhere possibly could partly offset the deficit in production at Necker. Our observations on the size distribution of egg production at Necker Bank nonetheless merit important consideration for setting size limits for spiny lobster management.

By necessity we calculated the IRP assuming that all size classes produced the same (single) brood per spawning period because data on size-specific spawning frequency were lacking. We caution that, if females >60 mm TW (whose size-specific egg production is greatest) produce broods more frequently than smaller females (Lipcius, 1985), we have proportionately underestimated the contribution of larger females to population egg production.

Individual *Panulirus marginatus* of all sizes likely produce multiple broods per individual spawning season, based on the protracted period during which females are berried (Uchida and Tagami, 1984; Polovina and Moffitt, 1995) and the occasional presence of new, intact (unused) spermatophore plates on spent females (unpubl. data, Honolulu Laboratory, NMFS). (The latter observation in fact suggests that Necker Bank *P. marginatus* can produce more than one brood per molt [like *P. argus*; Sutcliffe, 1953].) There are no time-series growth-rate data available with which to evaluate whether females of a given body size might now be producing larger broods at more frequent intervals than previously. If females are now growing faster, it is likely that the rates of both molting and brood production are now greater. Accurate estimates of individual spawning frequencies and how these might differ among females of varying body sizes, would be needed to fully describe the compensatory increase in reproduction which has occurred for the Necker Bank population of *P. marginatus*.

Acknowledgments

We thank several anonymous fishery observers for collection of invaluable commercial catch data and R. Moffitt, J. Polovina, and an anonymous reviewer for constructive criticisms of the manuscript.

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[2] DiNardo, G. T., W. R. Haight, and J. A. Wetherall. 1998. Status of lobster stocks in the Northwestern Hawaiian Islands, 1995–97, and outlook for 1998. Southwest Fish. Sci. Cent. Admin. Rep. H-98-05, 35 p. Honolulu Laboratory, Southwest Fish.Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.

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Appendix A

Two body size metrics (carapace length, CL; tail width, TW) and fecundity (F, number of brooded eggs) data for 40 individual spiny lobster (*Panulirius marginatus*) collected during 1999 at Necker Bank, Northwestern Hawaiian Islands. Data are ordered by increasing CL.

CL	*TW*	*F*
54.3	39.3	124,860
57.3	39.3	110,815
59.3	40.9	125,324
59.8	41.9	109,865
60.6	39.7	116,385
60.6	48.2	271,153
60.7	40.8	136,116
62.6	43.2	168,210
62.7	42.8	136,786
64.0	43.8	203,026
64.8	43.8	118,303
66.6	45.5	149,753
68.4	46.7	216,477
69.0	46.4	229,561
69.9	48.5	215,502
70.9	47.2	206,099
74.1	50.7	245,037
76.8	51.7	271,830
78.8	52.2	250,885
79.8	49.4	255,240
80.5	54.4	245,510
80.6	54.6	360,611
80.8	53.6	355,366
82.1	54.5	339,466
83.0	54.2	342,488
84.6	56.0	381,494
85.5	59.1	345,755
86.6	57.8	417,662
87.2	56.6	371,609
88.5	60.8	372,148
89.5	55.2	382,667
90.4	58.7	409,864
93.2	60.8	431,027
94.9	60.3	420,458
95.3	63.2	364,508
97.0	63.7	494,282
97.6	61.3	545,059
98.0	62.6	525,173
103.4	66.0	590,530
105.4	67.4	479,197

Impact of hatchery releases on the recreational fishery for Pacific threadfin (*Polydactylus sexfilis*) in Hawaii

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Abstract—The Pacific threadfin (*Polydactylus sexfilis*) is considered one of the premier Hawaiian food fishes but even with catch limits, seasonal closures, and size limits, catches have declined dramatically since the 1960s. It was identified as the top candidate species for stock enhancement in Hawaii, based on the decline in stocks, high market value, and importance of the fishery.

In the stock enhancement program for Pacific threadfin, over 430,000 fingerlings of various sizes were implanted with coded wire tags and released in nursery habitats along the windward coast of Oahu between 1993 and 1998. Because few Pacific threadfin were present in creel surveys conducted between 1994 and 1998, Oahu fishermen were offered a $10 reward for each threadfin that was caught (for both hatchery-reared and wild fish). A total of 1882 Pacific threadfin were recovered from the reward program between March 1998 and May 1999, including 163 hatchery-reared fish, an overall contribution of 8.7% to the fishery. Hatchery-reared fish accounted for as high as 71% of returns in the release areas. Hatchery-reared fish were recovered on average 11.5 km (SD=9.8 km) from the release site, although some had moved as far away as 42 km. Average age for recovered hatchery-reared fish was 495 days; the oldest was 1021 days.

Cultured Pacific threadfin juveniles survived and recruited successfully to the recreational fishery, accounting for 10% of fishermen's catches on the windward side of Oahu. Recruitment to the fishery was highest for the 1997 release year; few juveniles from earlier releases were observed. Presence of a few large, fully developed females in the recreational fishery suggested that hatchery-reared fish can survive, grow, and reproductively contribute to the population. Implementation of an enhancement program that is focused on juveniles and perhaps large females, as part of an integrated fishery management strategy, could speed the recovery of this fish population.

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Fish. Bull. 101:32–43 (2003).

Declining marine fish stocks worldwide have led to an increased interest in marine fish stock enhancement (Blankenship and Leber, 1995; Schramm and Piper, 1995; Leber et al., 1996; Grimes, 1998; Howell et al., 1999). Stock enhancement of marine fishes has progressed since the late 1800s and several successful marine fish stock enhancement programs have been documented; however, nearly all have been directed toward temperate species such as chum salmon (Kaeriyama, 1996), Japanese flounder (Kitada et al., 1992), red sea bream (Imai et al., 1994; reviewed by Masuda and Tsukamoto, 1998), and red drum (McEachron and Daniels, 1995; McEachron et al., 1998). In one successful marine fish stock enhancement program in the tropics, hatchery-reared striped mullet (*Mugil cephalus*) successfully recruited to the fishery, accounting for 13% of the commercial mullet catch in Kaneohe Bay, Hawaii (Leber and Arce, 1996).

The Pacific threadfin (*Polydactylus sexfilis*), known locally as "moi," is the only representative of the threadfin family (Polynemidae) in Hawaii (Randall, 1996). The distribution of Pacific threadfin extends throughout the Indo-Pacific region from Madagascar (Bleeker, 1875) to the Ogasawara Islands of southern Japan, east to Hawaii and south to the Tuamotu Archipelago (Randall et al., 1990; Myers, 1991). In ancient Hawaiian culture, Pacific threadfin were reserved for the ruling chiefs and prohibited for consumption by commoners (Titcomb, 1972). Pacific threafin were formerly harvested commercially, but commercial catches have declined steadily since the 1950s and have essentially ceased since 1968 when the daily catch limit was restricted to 15 fish per person. This decline in abundance, particularly around the more populated areas of the state, is likely the cumulative result of years of chronic overfishing (Shomura[1]). Current regulations comprise the following: a catch limit of 15 fish per person per day; a minimum fish size of 7 inch. TL (ca. 14.5 cm FL) for caught fish; and a closed season from 1 June to 30 September.

Pacific threadfin are typically found over shallow sand flats, along high wave-energy rocky shorelines, and in sandy beach wash zone habitats (Hosaka, 1990; Leber et al., 1998). They can also be found in turbid water near stream mouths and brackish mangrove estuaries (Randall et al., 1990; Myers, 1991). Local fishermen call areas where adult Pacific threadfin congregate "moi holes" (Hosaka, 1990); these usually occur in shoreline caves or sandy depressions and sand channels in the surf zone among boulders or reef areas.

Pacific threadfin are protandric hermaphrodites, initially maturing as males after a year at about 20–25 cm; they then undergo a sex reversal, passing through a hermaphroditic stage and becoming functional females between 30 and 40 cm FL at about three years of age (Santerre and May, 1977; Santerre et al., 1979; Szyper et al., 1991). Spawning occurs inshore

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[1] Shomura, R. 1987. Hawaii's marine fishery resources: yesterday (1900) and today (1986). Admin. Rep. H-87-21, 14 p. U.S. Dep. Commer., NOAA, NMFS, Southwest Fisheries Science Center, Honolulu, Hawaii 96822.

Table 1

Summary of Pacific threadfin (*Polydactylus sexfilis*) releases on the windward side of Oahu Island, 1993–97. Release size is fork length in mm.

Release year	Release sites	No. of fish released	Adjusted no. of fish released	% tag retention	Release size range (mm)
1993	Kahana	10,020	9939	99.2	70–150
	Laniloa	9990	9858	98.7	
1994	Kahana	40,530	37,888	93.5	48–130
	Malaekahana	40,695	37,561	92.3	
1996	Kahana	31,258	30,164	96.5	85–130
	Kailua	14,952	14,223	95.1	
1997	Kahana	99,020	96,019	97.0	70–130
	Kailua	97,569	94,349	96.7	
1998	Kahana	75,687	71,672	94.7	70–130
	Kailua	11,273	10,827	96.1	
Totals		430,994	412,500		

and eggs are dispersed and hatched offshore (Lowell, 1971). Larvae and juveniles are pelagic up to about 6 cm FL, at which size they enter inshore habitats including surf zones, reefs, and stream entrances (Santerre and May, 1977; Santerre et al., 1979). Newly settled young Pacific threadfin, locally called "moi-lii" (Lowell, 1971; Tinker, 1982), appear in shallow waters in summer and fall where they are the dominant member of the nearshore surf zone fish assemblage (Ziemann et al.[2]).

Pacific threadfin is a popular and much sought-after sport fish that also supports a small subsistence fishery in Hawaii (Santerre et al., 1979; Leber et al., 1998). It is presently an important species in the Hawaii recreational fishery because of its reputation as one of the best tasting fishes in Hawaii (Hosaka, 1990) and its high market value (wholesale market price over US$3.00 per kilogram). A species prioritization study conducted early in the stock enhancement research program in Hawaii identified Pacific threadfin as the top candidate for stock enhancement, based partly on the decline of its stocks, its high market value, and importance in the recreational fishery (Oceanic Institute[3]). As part of the Stock Enhancement of Marine Fish in the State of Hawaii (SEMFISH) program funded by the National Marine Fisheries Service, juvenile Pacific threadfin were released in nursery habitats along the windward coast of Oahu between 1993 and 1997 to evaluate the contribution of hatchery-reared fish to the local fishery. Leber et al. (1998) demonstrated site-specific potential success in stocking programs for juveniles in 1993–94. The purpose of this article is to provide long-term tracking of catches to determine the contribution of hatchery-produced fish versus wild stocks in the recreational fishery on the windward side of Oahu.

Methods

The culture of Pacific threadfin at the Oceanic Institute (OI) is described by Ostrowski et al. (1996). Most fish were released into coastal waters between day 60 for small juveniles (70–85 mm FL) and day 90 for larger juveniles (130–150 mm FL).

During each of five release years, 10,000 to 100,000 juveniles (per release site) were sorted by size and released in multiple lots over 3–5 months; the total number released per release site usually varied between years (Table 1, Fig. 1). Over the five release years, a total of 430,994 Pacific threadfin fingerlings were released. Before release, all fish received coded wire tags (Northwest Marine Technology, Inc., Shaw Island, WA: Jefferts et al., 1963) in the snout area to identify release lots by release size, date, and location. Approximately 5% of each release lot was retained in culture at OI to determine tag retention rates. Fish were examined monthly from 1 to 6 months until tag loss rates stabilized (i.e. when the number lost had not increased since the previous month). Tag retention rates varied from 93% to 99%. All calculations of tag recovery rates were based on coded–wire-tag data adjusted for tag retention rates.

We conducted a roving creel survey, encompassing all release areas, intermittently from 1994 to 1998 on the windward side of Oahu 1) to determine if released Pacific threadfin were surviving and being caught in the fishery, 2) to estimate Pacific threadfin CPUE in the recreational fishery, and 3) to inform fishermen about the Pacific threadfin

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[2] Ziemann, D. A., A. M. Friedlander, and P. Craig. 1998. Enhancement of Pacific threadfin *Polydactylus sexfilis* in Hawaii. I. Release optimization. Stock Enhancement of Marine Fish in the State of Hawaii (SEMFISH), Phase IX, 152 p. Oceanic Institute, 41-202 Kalanianaole highway, Waimanalo, HI 96795.

[3] Oceanic Institute. 1989. Selection of marine finfish species for stock enhancement in Hawaiian waters, 78 p. The Oceanic Institute, Makapuu Point, 41-202 Kalanianaole Highway, Waimanalo, HI 96795.

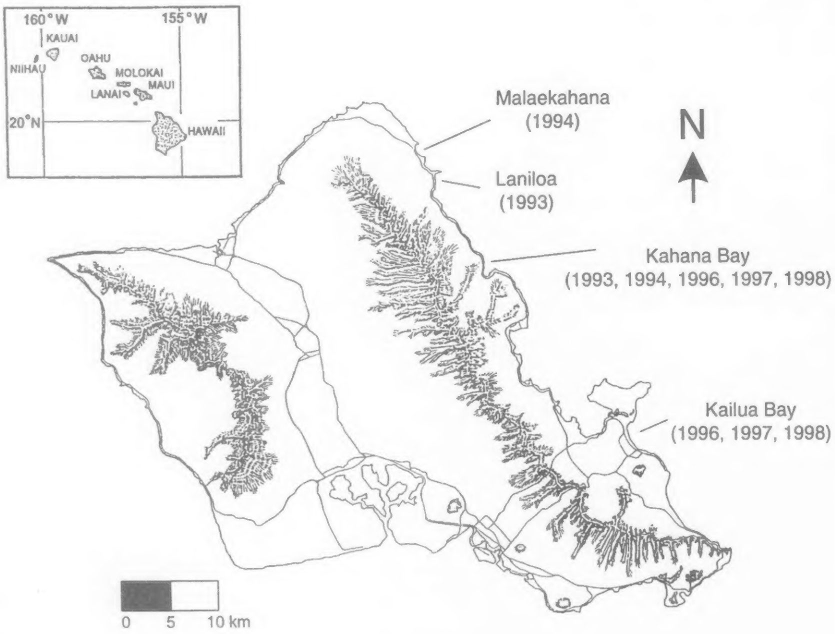

Figure 1

Island of Oahu, Hawaii showing locations for releases of hatchery-reared Pacific threadfin (*Polydactylus sexfilis*) from 1993 to 1998.

enhancement program. Fishermen were interviewed at boat docks and along the coastline to collect information about their catch and effort (species, lengths, number of hours fished per gear type). All Pacific threadfin in the catches were scanned for coded wire tags with a hand-held Northwest Marine Technologies cwt sensor ("wand").

Because Pacific threadfin were scarce in creel samples, we offered a $10 reward to Oahu fishermen for each Pacific threadfin (hatchery-reared and wild) caught in the open season between March 1998 and May 1999 (no retention is allowed from June to September). Posters, newspaper articles, and radio talk shows were used to publicize the reward program. We also informed participating fishermen that we were primarily interested in samples from the windward side of the island; thus, catches of Pacific threadfin from other parts of the island were underrepresented in our effort. To obtain the reward, fishermen provided date, location, gear used, fork length, and the head of each Pacific threadfin caught. Beginning in September 1998, fishermen had to return whole fish to obtain the $10 reward. This requirement allowed us to gather more accurate length information, as well as information on weight, sex, and gonadal condition. We obtained a relatively unbiased random sample from the fishery because fishermen were unable to determine visually whether a fish had a coded wire tag; this unbiased sample enabled us to calculate the contribution of hatchery-reared fish to the fishery.

A Mann-Whitney rank sum test (T-statistic) was used to compare distance traveled among sites and years for hatchery-reared fish. This test was also used to compare fork lengths of wild fish by sex between the 1999 and the 1962–68 sampling periods. We compared number of Pacific threadfin recovered in each size class in relation to the number of hatchery-reared fish released in that size class by using chi-square goodness of fit. Expected number of fish recaptured in each size class was calculated by taking the total number of recaptures for each year from each release site and multiplying it by the proportion of fish released in that size class at that site during that year.

A Kruskal-Wallis ANOVA on ranks with Dunn's multiple comparison procedure (Sokol and Rohlf, 1981) was used to identify pair-wise difference in CPUE among gear types; $\alpha = 0.05$. A two-way ANOVA (F) was conducted to compare fish length among gear types for wild and hatchery-reared Pacific threadfin during each reward year. Tukey multiple comparison procedures were conducted to determine pair-wise differences in fish length between gear types; $\alpha = 0.05$. Condition factor was calculated as

$$C = (W/L^3) \times 10{,}000,$$

where C = condition factor;
W = fish weight in grams; and
L = fork length in mm (Anderson and Neumann, 1996).

Table 2

Results of catch and effort from recreational creel surveys for Pacific threadfin conducted along the windward coast of Oahu between 1994 and 1998.

Gear type	Number of interviews	Total effort (h)	Number of threadfin	CPUE (number/h)	Number of hatchery-reared threadfin	Proportion hatchery-reared
Angling	464	3647	123	0.03	40	0.33
Gillnet	22	327	35	0.11	1	0.03
Throw net	42	93	3	0.03	0	0.00
Spear	23	81	0	0.00	0	0.00
Total	551	4148	161	0.04	41	0.25

Table 3

Summary of wild and tagged Pacific threadfin obtained from the recreational fishery from March 1998 to May 1999.

	1998				1999				Total			
Region	Hatchery-reared	Wild	Total	Proportion hatchery-reared	Hatchery-reared	Wild	Total	Proportion hatchery-reared	Hatchery-reared	Wild	Total	Proportion hatchery-reared
Ewa	0	18	18	0.00	0	0	0	0.00	0	18	18	0.00
Kahana	2	15	17	0.12	6	129	135	0.04	8	144	152	0.05
Kailua	35	14	49	0.71	4	6	10	0.40	39	20	59	0.66
Kaneohe	5	85	90	0.06	28	221	249	0.11	33	306	339	0.10
Laie	11	237	248	0.04	17	373	390	0.04	28	610	638	0.04
Mokapu	0	13	13	0.00	34	317	351	0.10	34	330	364	0.09
Mokuleia	0	8	8	0.00	0	0	0	0.00	0	8	8	0.00
North Shore	3	121	124	0.02	0	3	3	0.00	3	124	127	0.02
Sandy Beach	1	32	33	0.03	0	9	9	0.00	1	41	42	0.02
Waianae	0	18	18	0.00	0	0	0	0.00	0	18	18	0.00
Waimanalo	9	16	25	0.36	8	84	92	0.09	17	100	117	0.15
Total	66	577	643	0.10	97	1142	1239	0.08	163	1719	1882	0.09

Condition factors between sites and among release size classes were compared by using a two-way ANOVA (F); $\alpha = 0.05$. A Mann-Whitney rank sum test (T) was used to compare the gonadosomatic index (GSI=ovary weight/body weight×100) between hatchery-reared and wild Pacific threadfin recovered in the 1999 reward program.

Results

CPUE for Pacific threadfin from 551 creel survey interviews of recreational fishermen from 1994 to 1998 was very low (0.04 fish/h for all gear types combined) (Table 2): 1 per 33 hours by angling or 1 per 9 hours by gillnet. These values are probably low estimates because the creel survey was not directed at fishermen who targeted Pacific threadfin. Even though we saw a very small number of Pacific threadfin in the creel surveys, hatchery-reared fish made up 33% (40 of 123) of the angling catch and 25% (41 of 161) of the overall catch.

The voluntary reward program between March 1998 and May 1999 yielded 1882 Pacific threadfin (Table 3), of which 163 were hatchery-reared Pacific threadfin (8.7%). The period March–May 1998 provided 643 Pacific threadfin, compared to 1239 for the period September 1998–May 1999. Tag information was readable for 63 of 66 fish recovered in 1998 (3 damaged tags) and all 97 tags recovered in 1999. Of the total readable tags, fish released in 1997 made up 93.7% (n=59) of the 1998 reward fish and 95.9% (n=93) of the 1999 reward fish. Four fish from 1996 releases were recovered in each year. Although most fish recovered in the reward program were from the windward or eastern side of Oahu, 168 fish (26.1%), including 4 hatchery fish from the North Shore area, did come from other areas around the island in 1998 (Fig. 2). Three reward fish were returned from the North Shore in 1999. No hatchery-

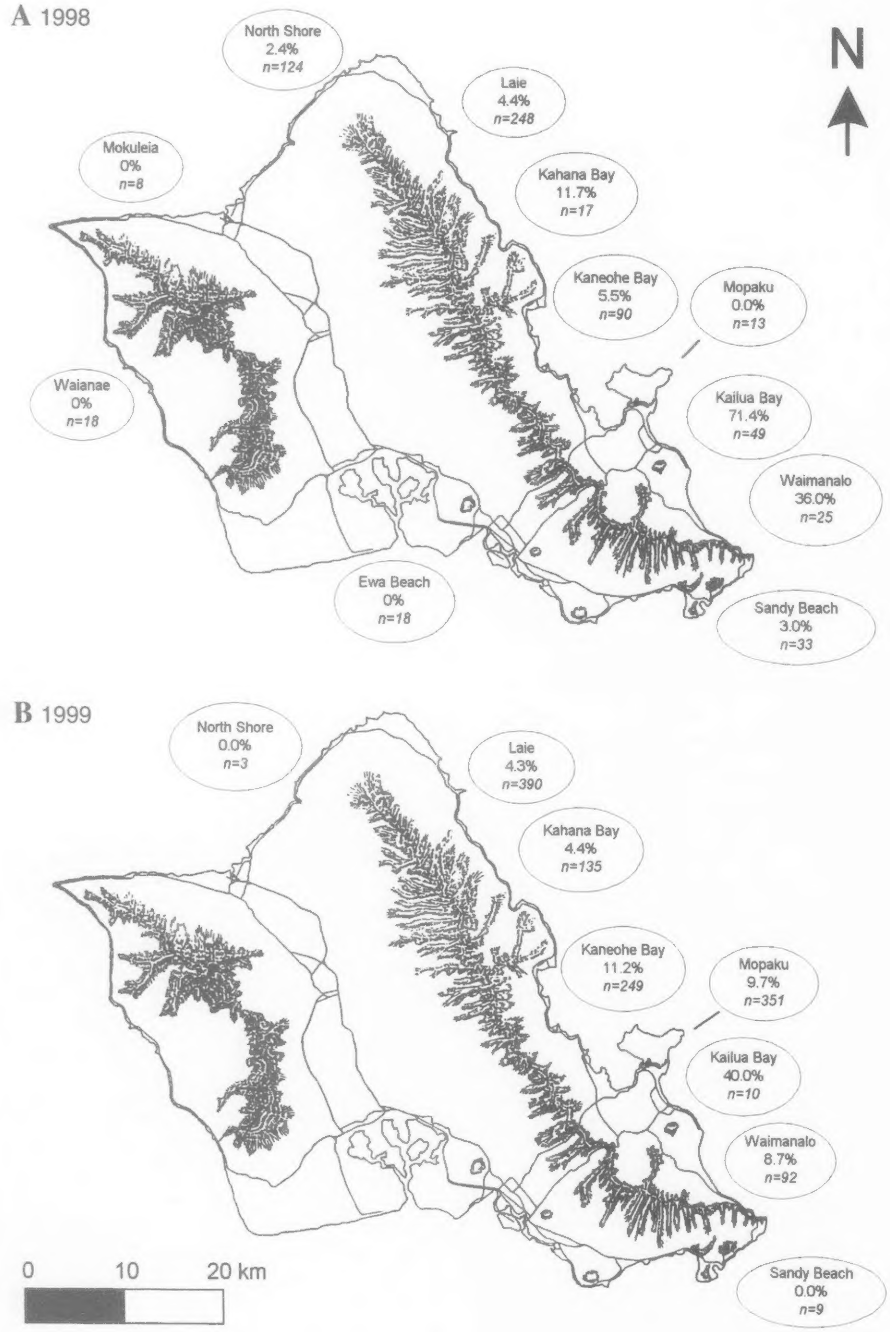
A 1998
N
North Shore
2.4%
n=124
Laie
4.4%
n=248
Mokuleia
0%
n=8
Kahana Bay
11.7%
n=17
Kaneohe Bay
5.5%
n=90
Mopaku
0.0%
n=13
Waianae
0%
n=18
Kailua Bay
71.4%
n=49
Waimanalo
36.0%
n=25
Ewa Beach
0%
n=18
Sandy Beach
3.0%
n=33
B 1999
North Shore
0.0%
n=3
Laie
4.3%
n=390
Kahana Bay
4.4%
n=135
Kaneohe Bay
11.2%
n=249
Mopaku
9.7%
n=351
Kailua Bay
40.0%
n=10
Waimanalo
8.7%
n=92
0
10
20 km
Sandy Beach
0.0%
n=9

Figure 2

Percentage of hatchery-reared Pacific threadfin recovered from the recreational reward fishery program during the (**A**) 1998 and (**B**) 1999 fishing seasons. n = the total number of Pacific threadfin recovered at each site.

Table 4

Number of 1997 released fish obtained from the reward fishery for the years 1998 and 1999. Expected values were derived from the total number of hatchery-reared fish returned during each reward year from each release site, multiplied by the proportion of fish released in each size class. No χ^2 value was significant at $P < 0.05$.

Release size (mm)	Adjusted no. of fish released	1998		1999	
		Hatchery-reared	Expected	Hatchery-reared	Expected
Kahana					
70–85	14,152	5	2.51	8	5.45
85–100	34,618	5	6.14	16	13.37
100–115	41,069	6	7.27	11	15.83
115–130	6,102	1	1.08	2	2.35
Total	96,019	17	17.00	37	37.00
χ^2			2.91		3.24
Kailua					
70–85	15,415	9	6.86	14	9.15
85–100	35,090	19	13.62	17	20.83
100–115	37,819	14	16.84	25	22.45
115–130	6,022	0	2.68	0	3.57
Total	94,349	42	42.00	56	56.00
χ^2			4.56		7.14

reared fish were recovered from the leeward coast or south shore areas. Highest proportions of hatchery-to-wild fish were found in Kailua Bay (71%) and at Waimanalo Beach (36%) during the 1998 season. For the Kahana Bay site, around 12% of the Pacific threadfin recovered in the 1998 reward program were hatchery-reared. For the 1999 reward program, Kailua Bay continued to have the highest percentage of hatchery-reared Pacific threadfin, 40%. Hatchery-reared Pacific threadfin were also recovered at Waimanalo Beach (8.7%), Mokapu Peninsula (9.7%), and Kaneohe Bay (11.2%); the latter two sites are north of the Kailua Bay release site.

Hatchery-reared Pacific threadfin released in Kahana Bay were recovered as far north as Kawela Bay (25 km) and south to Waimanalo Beach (33 km) (Fig. 3). Fish released in Kailua Bay were recovered 19 km to the south at Sandy Beach and 42 km to the north at Kahuku (Fig. 4). Fish were captured at significantly greater distances from the release sites in 1999 ($\bar{x}$=15.2 km, SD=10.2) than in 1998 ($\bar{x}$=11.0 km, SD=6.8) (T=2044.0, P=0.025). Fish released in Kahana Bay were recaptured at significantly greater distances from the release site ($\bar{x}$=14.6 km, SD=11.0) compared to the Kailua Bay releases ($\bar{x}$=9.6 km, SD=6.3; T=6129.0, P<0.001).

The proportion of fish recaptured in the reward program for 1998 and 1999 was lowest in the largest release size class (115–130 mm) and greatest in the middle two release size classes (85–100; 100–115 mm). Because the number of fish released in each size class in 1997 was different, it was necessary to compare the number of fish recovered in each size class in relation to the number released in that size class. Eight fish recaptured from the 1996 release were not included in our analyses. For both years and both locations, the catch of hatchery-reared Pacific threadfin divided by the adjusted release number was greatest in the smallest size class (70–85 mm) (Table 4).

Expected number of fish recaptured in each size class was calculated by taking the total number of recaptured fish for each year from each release site and multiplying it by the proportion of fish released in that size class at that site during that year (Table 4). There were no significant differences in number of fish recaptured in each size class in relation to expected recapture numbers for both years at the Kahana Bay release site (1998: χ^2=2.91, df=3, P>0.05; 1999: χ^2=3.24, df=3, P>0.05) and for Kailua Bay (1998: χ^2=5.74, df=3, P>0.05; 1999: χ^2=7.14, df=3, P>0.05).

Angling (pole and line fishing) accounted for the greatest number of hatchery-reared and wild Pacific threadfin acquired in the reward program but had the lowest CPUE among gear types (Table 5). Over both survey years, for wild and hatchery-reared fish combined, angling accounted for 63.0% of the total Pacific threadfin catch, followed by gillnets (19.2%), thrownets (13.9%), and surround nets (3.9%).

Length of Pacific threadfin caught varied among gear types, between years, and between hatchery-reared and wild Pacific threadfin. For 1998, mean size of Pacific threadfin captured was significantly different among gear types (F=6.378, df=3, 632, P<0.001) and between hatchery-reared and wild fish (F=11.833, df=1, 632, P<0.001). Gillnets tended to catch larger fish, and surround nets captured the smallest fish (Tukey multiple comparison test results—gillnets: 255.5 mm ≥ angling: 235.1 mm ≥ thrownet: 214.0 mm > surround nets: 193.7 mm). Mean length for hatchery-reared Pacific threadfin pooled over all gear types was 207.0 mm (SD=28.6) and mean length for wild Pacific threadfin was 242.2 mm (SD=52.7).

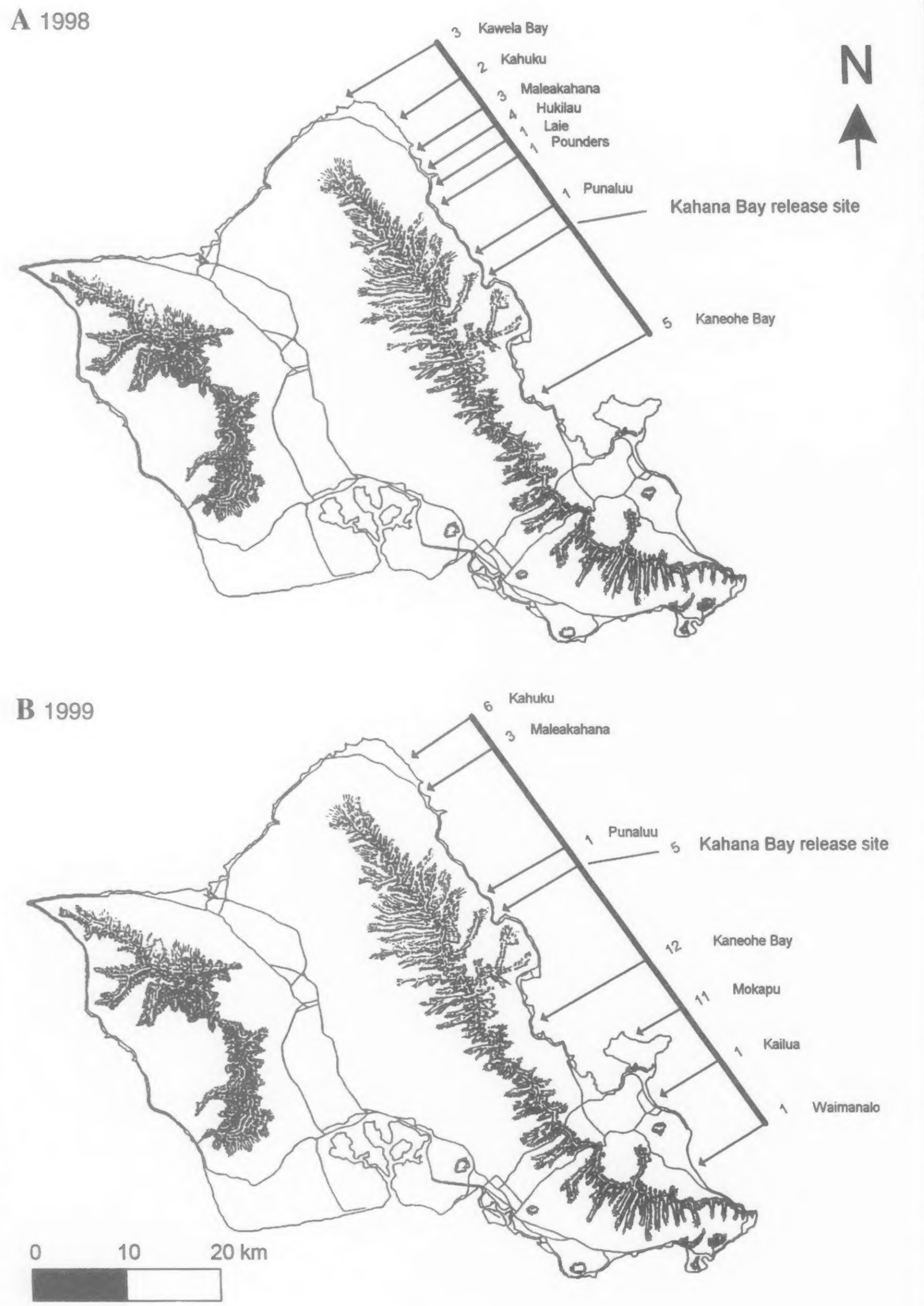
A 1998
3 Kawela Bay
2 Kahuku
3 Maleakahana
4 Hukilau
1 Laie
1 Pounders
1 Punaluu
Kahana Bay release site
5 Kaneohe Bay
N
B 1999
6 Kahuku
3 Maleakahana
1 Punaluu
5 Kahana Bay release site
12 Kaneohe Bay
11 Mokapu
1 Kailua
1 Waimanalo
0 10 20 km

Figure 3

Movement patterns of hatchery-reared Pacific threadfin released in Kahana Bay from the reward fishery program during the (**A**) 1998, $n = 20$ and (**B**) 1999, $n = 40$ fishing seasons.

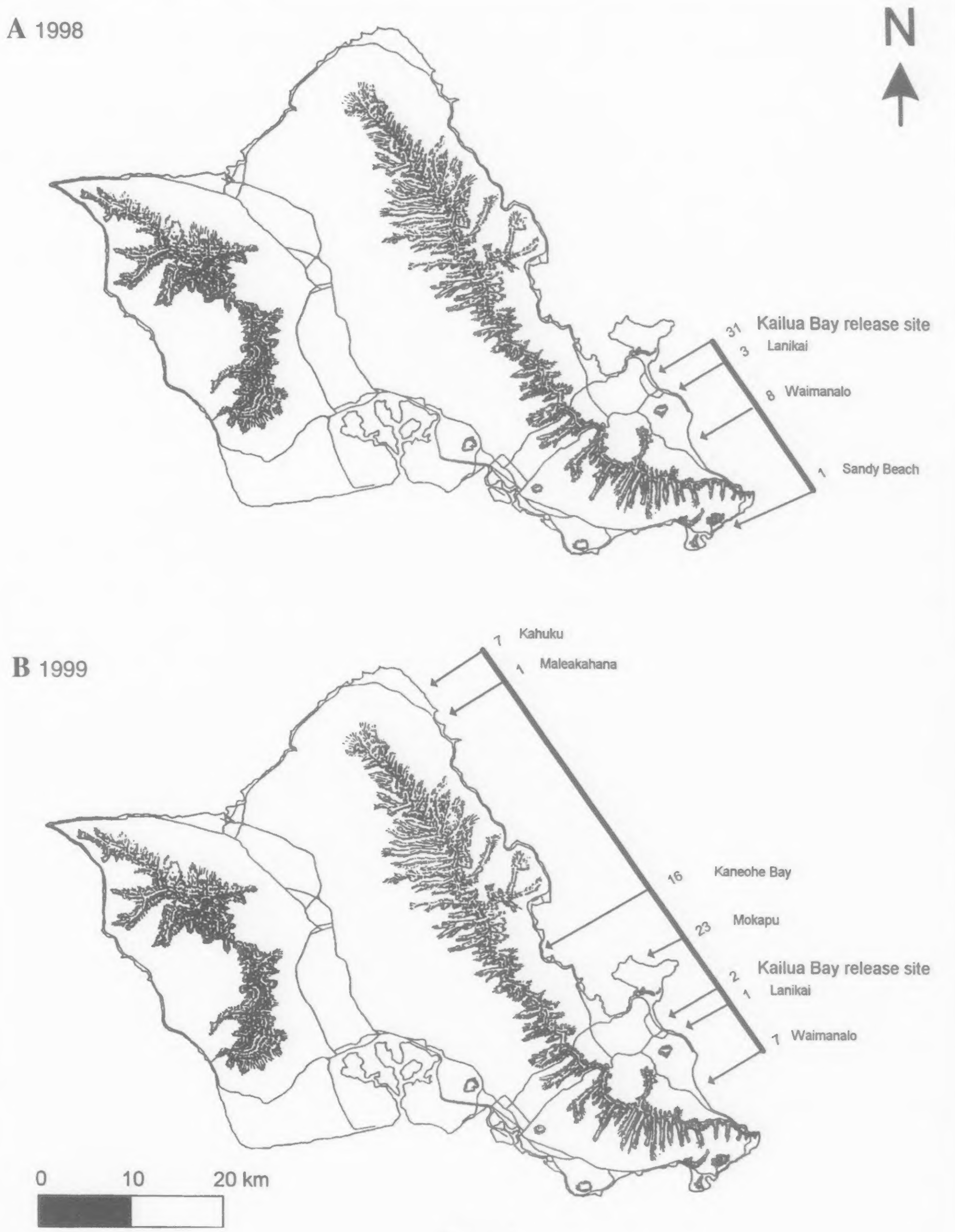
A 1998
N
31 Kailua Bay release site
3 Lanikai
8 Waimanalo
1 Sandy Beach
B 1999
7 Kahuku
1 Maleakahana
16 Kaneohe Bay
23 Mokapu
2 Kailua Bay release site
1 Lanikai
7 Waimanalo
0 10 20 km

Figure 4

Movement patterns of hatchery-reared Pacific threadfin released in Kailua Bay from the reward fishery program during the (**A**) 1998, $n = 43$ and (**B**) 1999, $n = 57$ fishing seasons.

Information on sex of Pacific threadfin obtained in the reward program was available only during 1999 because whole fish were not acquired in 1998. The ratio of male to hermaphrodite to female was 56:17:27 for wild Pacific threadfin and 81:15:4 for hatchery-reared fish (Fig. 5). Three hatchery-reared fish that had changed from males

Table 5

Catch per unit of effort (CPUE) for Pacific threadfin caught by three different gear types used in the recreational-artisanal fishery. Mean rank computed for Kruskal-Wallis rank sum test (H=19.303, df=2, P<0.001). Results of Dunn's multiple comparison procedure. Gear types with the same letter (A, B) are not significantly different.

Gear type	n	Total hours	Total no. of threadfin	No hatchery-reared	Mean CPUE	SD CPUE	Dunn's multiple comparisons
Thrownet	16	55.0	166	7	5.49	9.34	A
Gillnet	31	83.5	221	20	3.52	4.89	A B
Angling	113	592.5	817	56	1.63	1.44	B
Grand total	160	731.0	1204	83	2.38	3.98	

Table 6

Comparison of size (mm FL) and sex for hatchery-reared and wild catch Pacific threadfin acquired from the reward fishery in 1999.

	Hatchery-reared				Wild			
Sex	Mean	Min.	Max.	n	Mean	Min.	Max.	n
Males	257.1	210	307	61	250.0	174	360	372
Hermaphrodites	267.2	220	323	11	275.0	200	380	112
Females	311.3	247	356	3	315.6	249	462	179

to females were recovered during 1999; one was released during summer 1996, the other two were released during summer 1997.

Mean size for males was 250.0 mm (SD=32.1) for wild fish and 257.1 mm (SD=24.8) for hatchery-reared fish; mean size for hermaphrodites was 275.0 mm (SD=27.5) for wild fish and 267.2 mm (SD=43.3) for hatchery-reared fish; mean size for females was 315.6 mm (SD=39.2) for wild Pacific threadfin and 311.3 mm (SD=57.1) for hatchery-reared threadfin (Table 6). The GSI for hatchery-reared males (x=0.629, SD=0.728) was not significantly different (T=6524, P=0.073) than the GSI for wild males (x=0.619, SD=0.842), likely because of the larger size of hatchery-reared males during 1999. Number of hatchery-reared females and hermaphrodites was too low for statistical comparisons.

Condition factor for hatchery-reared Pacific threadfin during 1999 was not significantly different between release sites (F=0.074, df=1, 79, P=0.786) or among release sizes (F=1.488, df=3, 79, P=0.224). Therefore, condition factors for all hatchery-reared fish were pooled and compared to condition factors for all wild fish recovered in 1999. No significant difference was found in condition factors between these two groups (T=47733.0, P=0.087).

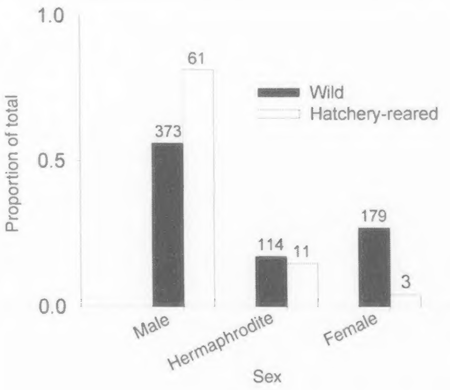

Figure 5

Sex ratio for wild and hatchery-reared Pacific threadfin returned for the 1999 reward fishing season. Values are total number of fish in each sex category.

Discussion

Cultured Pacific threadfin juveniles released into the ocean survived and recruited successfully into the recreational fishery, accounting for 10% and 8% of the catch on the windward side of the island of Oahu in two years (1998 and 1999, respectively). Hatchery fish from the 1997 release constituted the majority of the hatchery fish returns to the recreational fishery in 1998 (89.4%) and 1999 (95.9%). Few of the hatchery fish released in years prior to 1997 have been recovered from the recreational fishery. The large

Table 7

Comparisons of length of juveniles, males, hermaphrodites, and females for Pacific threadfin around Oahu from 1962 to 1968 and for wild fish from the 1999 reward fishery program. One standard deviation of mean fork length is shown in parentheses.

	1962–68, n=1651		1999 reward program, n=1105			
Sex	Fork length (mm)	Percentage of total	Fork length (mm)	Percentage of total	Mann Whitney T-value	P
Juveniles	227 (30)	6.4	191 (24)	39.7	44864	<0.001
Males	268 (29)	52.3	249 (35)	33.8	184831	<0.001
Hermaphrodites	317 (33)	17.8	275 (27)	10.3	11952	<0.001
Females	378 (45)	23.5	316 (39)	16.2	26200	<0.001

impact of a relatively small number of released fish on the recreational fishery shows that hatchery releases of limited numbers of fish have the potential to impact both the number of fish taken in the fishery and the rate at which the fishery can recover. The differences in contribution rates for different release years suggest that natural factors affecting the survival of juveniles, as well as early larval stages, vary between years.

Hatchery-reared and released fish collected in the recreational fishery showed growth rates, condition factors, and gonadosomal indices similar to those of wild fish, suggesting that hatchery-reared fish are able to adapt to the natural environment and integrate into the wild population. Our data (unpubl.) for wild and hatchery fish collected in nursery habitats showed no significant differences in growth rates. The mean size of hatchery-reared fish collected in 1998 was smaller than in 1999 (over 95% of the fish collected in 1998 and 1999 came from the same releases in 1997). Mean size for hatchery-reared fish in 1999 was not different from the mean size of wild fish for both years, which suggests that size of hatchery fish in 1999 represents the approximate size of 2–3 year-old threadfin and mean age of fish in the recreational fishery is also 2–3 years. The size-frequency distributions of hatchery and wild fish in 1998 and 1999 suggest that a significant portion of the wild fish in the fishery is younger than two years.

Small hatchery fish at release made a higher relative contribution to the recreational fishery than did the larger size group (but not significantly so, except for fish taken in Kailua Bay in 1999), and the nursery habitat sampling conducted after the 1997 releases showed the same (Leber et al., 1998; Ziemann et al.[2]). This pattern is in contrast to that observed for mullet in Hawaii (Leber, 1995) and Pacific threadfin for other years (Ziemann et al.[2])

Hatchery fish disperse slowly from the point of release along the windward coast of Oahu. In nursery habitats three months after release (Ziemann et al.[2]), hatchery fish represented in excess of 70% of the threadfin and they decreased within nine months to 10% or less. Some decrease is due to predation, but some is due to dispersal because in 1998, after 1 year at large, fish were caught in the recreational fishery a mean distance of 11.2 km from the release point, and after two years, mean distance had increased to 15.2 km. Dispersal from the two release sites differed: after one year mean distance for Kahana Bay releases was 14.6 km, whereas mean distance for fish releases in Kailua Bay was 9.6 km.

The 1999 reward sample contained 16% females, 44% males and hermaphrodites, and 40% immature fish. The life cycle of Pacific threadfin (protandric hermaphrodites) makes this skewed sex ratio even more problematic because individuals do not become functional females until about 30 cm FL and these larger fish are selectively removed from the population by fishing. For protogynous species, size-selective fishing mortality may result in differential loss of larger males (Sadovy, 1996; Beets and Friedlander, 1999). The percentage of juveniles in the catch was high. Mean size of Pacific threadfin in all sexual categories was significantly smaller than that reported by Kanayama[4] in 1962–68 (Table 7, Fig. 6); further, females constituted 23.5% of the catch in the 1960s, but only 16.2% of the catch in 1999. We demonstrated that cultured Pacific threadfin juveniles released in known nursery habitats survive and recruit successfully into the recreational fishery 1–2 years later. Our Pacific threadfin data indicate that recruitment of young fish to the population may be jeopardized because there are few mature females left in the population (recruitment overfishing), even with supplementation of hatchery-reared fish.

The underlying problem of the threadfin fishery on Oahu and the other Hawaiian Islands is primarily an intense local harvest by subsistence and recreational fishermen, as well as habitat loss from coastal and upland development. Current state regulations, as well as unregulated removal of larger individuals from the population, contribute to the male-biased sex ratios observed in our study. Stock recovery based on natural reproduction will be a long-term process. Implementation of an enhancement program for Pacific threadfin focused on juveniles and perhaps larger females could speed the rate of recovery of the local population.

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[4] Kanayama, R. 1973. Life history aspects of the moi *Polydactylus sexfilis* in Hawaii, 50 p. State of Hawaii, Department of Lands and Natural Resources, Honolulu, Hawaii.

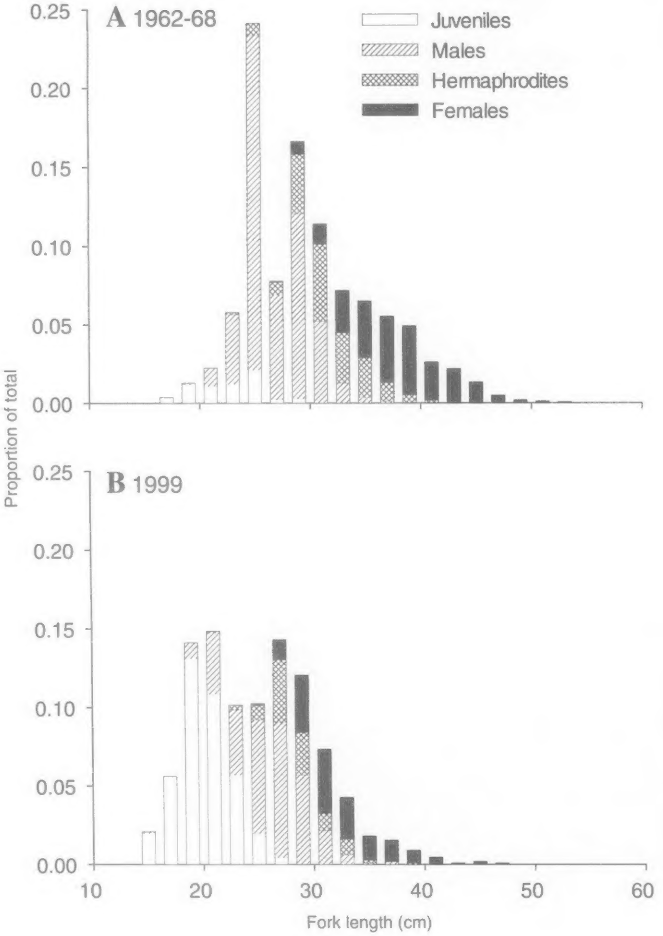

Figure 6

Proportion of juveniles, males, hermaphrodites, and females for Pacific threadfin from (**A**) 1962 to 1968 and (**B**) during the 1999 reward fishery program.

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Abstract—A general model for yield-per-recruit analysis of rotational (periodic) fisheries is developed and applied to the sea scallop (*Placopecten magellanicus*) fishery of the northwest Atlantic. Rotational fishing slightly increases both yield- and biomass-per-recruit for sea scallops at F_{MAX}. These quantities decline less quickly when fishing mortality is in-creased beyond F_{MAX} than when fishing is at a constant rate. The improvement in biomass-per-recruit appears to be nearly independent of the selectivity pattern but increased size-at-entry can reduce or eliminate the yield-per-recruit advantage of rotation. Area closures and rotational fishing can cause difficulties with the use of standard spatially averaged fishing mortality metrics and reference points. The concept of temporally averaged fishing mortality is introduced as one that is more appropriate for sedentary resources when fishing mortality varies in time and space.

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Yield- and biomass-per-recruit analysis for rotational fisheries, with an application to the Atlantic sea scallop (*Placopecten magellanicus*)

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There has been growing interest in using rotational fishing to manage sessile or sedentary stocks (e.g. Caddy and Seijo, 1998). Under such a strategy, fishing mortality in a given area is varied periodically. Typically, the area is closed for a period of time, then fished, and then closed again. The openings of the different areas are timed so that at least one area is open to fishing each year. This approach has been proposed or is being used for abalone, corals, sea cucumbers, geoduck clams, sea urchins, and several species of scallops (Sluczanowski, 1984; Garcia, 1984; Botsford et al., 1993; Caddy, 1993; Heizer, 1993; Campbell et al., 1998; Caddy and Seijo, 1998; Lai and Bradbury, 1998).

Recently, area closures have been used to help manage the Atlantic sea scallop (*Placopecten magellanicus*) fishery off the northeastern United States. Three areas on Georges Bank were closed to scallop and groundfish fishing in December 1994 to help protect depleted groundfish resources. Subsequently, there have been substantial increases in scallop abundance, biomass, and mean size in these areas; mean scallop biomass in the closed areas, as measured by the Northeast Fisheries Science Center (NEFSC) sea scallop survey, rose from 0.6 kg/tow in 1994 to 15.8 kg/tow in 2000.[1] During limited openings of these areas to fishing in 1999 and 2000, nearly 5000 metric tons (t) of scallop meats (about 20% of the total landings during this period) were landed, while biomass levels remained high. In April 1998, two areas in the Mid-Atlantic Bight were closed to scallop fishing for three years in order to protect high concentrations of juvenile scallops. Scallop biomass has increased markedly since the closures in these areas as well, from 0.8 kg/tow in 1997 to 9.7 kg/tow in 2000[1] and about 3500 t of scallop meats have been landed in these areas in the year since they were reopened in May 2001. These data suggest that temporary or rotational closures can help increase scallop biomass and yield. For these reasons, a rotational management system for the U.S. Atlantic sea scallop fishery is currently under consideration.

Many common fisheries models may not be appropriate for sessile stocks because these models assume spatially uniform fishing mortality (Caddy, 1975). Such a "dynamic pool" assumption is strongly violated when a sessile stock is fished rotationally so that a portion of the stock is not fished in a given year. For this reason, many previous analyses of rotational fisheries have used either spatially explicit simulations (e.g. Caddy and Seijo, 1998), per-recruit analyses of pulse fishing, where all vulnerable individuals are removed from an area when the area is fished (e.g. Sluczanowski, 1984), or per-recruit analyses of a single cohort (e.g. Gribble and Dredge, 1994). Spatially explicit models suffer from their complexity, making it difficult to extract general principles from model simulations. Analysis of pulse fishing, although simple to apply and understand, is not applicable to those situations where only a portion of the available resource is removed when an area is opened periodically to fishing. Per-recruit analysis of a single cohort is not applicable to relatively nonselective multiple age-group fisheries.

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[1] NEFSC (Northeast Fisheries Science Center). 2001. Report of the 32nd northeast regional stock assessment workshop (32nd SAW). Stock Assessment Review Committee (SARC) consensus summary of assessments. NEFSC Ref. Doc. 01-05, 289 p. [Available from NEFSC, 166 Water St., Woods Hole MA 02543.]

Botsford et al. (1993) developed a mixed-age rotational yield-per-recruit model for red sea urchins. They showed that rotational fishing for these urchins would increase egg production considerably, while slightly decreasing yield-per-recruit. Recently, Myers et al. (2000) presented a mixed-age per-recruit analysis of a possible rotational fishery strategy for sea scallops. The emphasis of this study was on the effect of putative high levels of indirect (noncatch) fishing mortality on yield-per-recruit, and on a proposed rotational plan that Myers et al. suggested would help ameliorate this effect.

The purpose of the present article is to present a general theory for any type of periodic or rotational fishing strategy for a mixed-age sessile or sedentary stock. This work generalizes many of the above mentioned studies (in particular, that of Botsford et al., 1993) and does not require an assumption of constant recruitment or specific spatial configuration (or both). This theory is applied to the Atlantic sea scallop fishery of Georges Bank.

Measures of fishing mortality and overfishing definitions are usually based on models where fishing is assumed constant in space and time. In rotational fisheries, or in cases where part of a fishing ground has been closed indefinitely to fishing, these assumptions may be seriously violated, especially for stocks that are relatively immobile. Alternative measures of fishing effort and overfishing definitions are presented here that are more appropriate to fisheries of nonmobile stocks where rotational or indefinite closures are used.

Methods

The object of this analysis was to compute the expected yield-per-recruit and biomass-per-recruit of a cohort located in an area where fishing mortality may depend on the year and the variation in fishing mortality is periodic with time. Rotational fishing is usually thought of as a sequence of periodic closures and openings of different areas. The theory described here is more general, and can be applied to any situation where fishing mortality is varied periodically in a given area.

Suppose the fully recruited fishing mortality in an area during year k is F_k and that fishing mortality rates vary periodically with period p (where p is in years), so that $F_{p+k} = F_k$ for all k. Let F_{AVG} be the mean of $F_1, F_2, \ldots, F_p$. For simplicity, it is assumed that there is one recruitment event and one new cohort per year. However, extension of the theory to multiple cohorts per year is straightforward.

There are p possible patterns of fishing mortality experienced by a cohort, depending on the point of the cycle when it enters the fishery. The cohort that enters in the first year will experience fully recruited fishing mortality rates:

$$F_1, F_2, F_3, \ldots, F_p, F_1, F_2, F_3 \ldots \tag{1}$$

during successive years. The next cohort will experience the same fishing mortality rates, but in a different order:

$$F_2, F_3, F_4, \ldots, F_p, F_1, F_2, \ldots \tag{2}$$

and so on.

Two special cases are of particular interest: pulse rotation and symmetric rotation. Pulse rotation means that $F_k = 0$ for $k=1,2,\ldots,p-1$ (the area is closed for $p-1$ years), then $F_p>0$ (the area is pulse fished for one year), and then $F_k=0$ for $k=p+1, p+2,\ldots, 2p-1$ (the area is closed again), etc. Symmetric rotation, where p is even, means that $F_k = 0$ for $1 \le k \le p/2$, and $F_k = 2F_{\mathrm{AVG}}$ for $p/2 < k \le p$, i.e. the area is closed for $p/2$ years and then fished at a constant rate for the next $p/2$ years.

For each of the p patterns of fishing mortality, yield- and biomass-per-recruit can be calculated by using standard per-recruit techniques. Here, a method similar to the "generic per-recruit" model described in Quinn and Deriso (1999) is used (see Appendix). The only unusual aspect is that the mortality terms Z and F_c in Equations 11–13 (see Appendix) depend explicitly on time, i.e. on the year of the rotational cycle. Each of the p cohorts will have different yield-per-recruit $Y_1, Y_2, \ldots, Y_p$, and biomass-per-recruit $B_1, B_2, \ldots, B_p$ values because the ages at which they experience the fishing mortalities $F_1, F_2, \ldots, F_p$ are different.

Define Y_{AVG} and B_{AVG} to be the means of the p patterns of cohort yield- and biomass-per recruit, respectively. Y_{AVG} is the expected yield of a recruit chosen randomly with respect to cohort. In other words, Y_{AVG} is the long-term mean yield-per-recruit that can be expected from the rotational fishing strategy. Similarly, B_{AVG} is the expected long-term mean biomass-per-recruit. Note that unlike conventional per-recruit theory, yield- and biomass-per-recruit vary with cohort, so that the mean yield- and biomass-per-recruit obtained at any point in time may be different from Y_{AVG} and B_{AVG}.

Let $Y^{(1)}, Y^{(2)}, \ldots, Y^{(p)}$ be yield-per-recruit of the p cohorts, in decreasing order, so that $Y^{(1)}$ is the highest yield-per-recruit out of all the p cohorts and $Y^{(p)}$ the lowest. $Y^{(1)}$ is an upper bound on the yield-per-recruit that might be obtained with a rotational strategy if, for example, the closure pattern were timed to optimize yield-per-recruit from a large year class.

It is important when comparing rotational and constant fishing strategies to compare alternatives that have the same long-term survival rates, i.e the same natural mortalities and mean fishing mortality rates. If this is not done, then effects of rotation can be confounded with those due to variations in fishing mortalities. If there are initially N_0 fully recruited individuals in an area that are fished at a constant rate F_u, then there will be

$$N_p = N_0 \exp(-pM - pF_u) \tag{3}$$

of these individuals remaining alive after p years. If instead, fishing mortality was varied on a p year rotation, so that in each year of the cycle, fishing mortality in an

Table 1

Estimated life history parameters for Georges Bank sea scallops. Von Bertalanffy growth parameters are from Serchuk et al. (1979). Relations of shell height (SH) to meat weight (MW) (see Eq. 7) were obtained by combining the data of Serchuk and Rak[1] with that of NEFSC (Footnote 2 in the general text). The natural mortality estimate is from Merrill and Posgay (1964). The selectivity pattern is based on the current gear configuration of scallop dredges with 89-mm rings (NEFSC, Footnotes 1 and 2 in the general text).

	K (/yr) (growth)	L_∞ (mm) (growth)	M (/yr) (natural mortality)	a (ln g) (SH/MW parameter)	b (SH/MW parameter)	$h_{\min}$ (mm) (Min SH selected)	h_{full} (mm) (SH for full selectivity)	h_d (mm) (cull size)	d (discard mortality)
Value	0.3374	152.46	0.1	–11.6038	3.1221	65	88	75	0.2

[1] Serchuk, F. M., and R. S. Rak. 1983. Biological characteristics of offshore Gulf of Maine scallop populations: size distribution, relations of shell height to meat weight, and relative fecundity patterns. Reference document 83-07, 42 p. [Available from Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.]

area is given by F_1, F_2, , F_p, respectively, then the number of individuals remaining alive after p years would be

$$N_p^* = N_0 \exp\left(-pM - \sum_{i=1}^{p} F_i\right). \tag{4}$$

In order for the long-term survivorship of the two strategies to be equal (i.e., $N_p = N_p^*$), the uniform fishing mortality F_u must equal the average fishing mortality

$$F_{AVG} = \frac{1}{p}\sum_{i=1}^{p} F_i \tag{5}$$

of the rotation plan. Therefore, F_{AVG} is used to scale all the graphs and per-recruit comparisons.

The model described above and in the Appendix was implemented as a Fortran-90 program where the integrals were numerically computed with a time step of 0.01 y. Parameters used in the model are given in Table 1 and represent estimates for growth and mortality of Atlantic sea scallops (*Placopecten magellanicus*), for which rotational management is currently under consideration.

Results

Yield-per-recruit curves for no rotation (continuous uniform fishing), three-year pulse rotation (i.e. the area is closed for two years and fished for one year), six-year pulse rotation, and nine-year pulse rotation are given in Figure 1. Note that the x axis in Figure 1 is the mean fishing mortality rate F_{AVG}, and the y axis is mean (i.e. expected) yield-per-recruit Y_{AVG}, averaged over cohorts. Because the mean fishing mortality rate is the same for all points at the same x coordinate, the three-year rotation has a fishing mortality rate during years when fishing occurs (F_p) that is three times as high, and the six-year rotation six times as high, as the constant F (no rotation) strategy with the same F_{AVG}.

Rotation affects the yield-per-recruit curve for sea scallop in three different ways (see Fig. 1). First, rotation modestly increases the maximum mean yield-per-recruit Y_{MAX}; the maximum mean yield-per-recruit for the nine-year rotation is about 9% greater than without rotation. Second, F_{MAX} (i.e. the value of F_{AVG} where Y_{MAX} is obtained) increases somewhat under rotation, especially for longer rotation periods. Third, there is less yield penalty in rotational management for exceeding F_{MAX}. For example, fishing at $F = 1$ results in a 38% loss of yield if there was no rotation, but only an 8% loss under a six-year pulse rotation. Although 6-yr pulse rotation results in only a 5% increase in yield-per-recruit over no rotation at their respective F_{MAX} values, the advantage of 6-yr pulse rotation at $F = 1$ is 43%.

Maximum yield-per-recruit for pulse fishing as a function of the rotation period p is shown in Figure 2. The best yield-per-recruit is obtained for long periods of 9 to 10 years. However, this type of strategy would imply that a number of years would pass before any yield would be obtained from most recruits and this strategy would only slightly increase maximum yield-per-recruit over that of steady fishing. Depending on management goals, it might be reasonable to discount future yields, so that the present value of yield taken t years into the future would be discounted by $\exp(-\delta t)$, where δ is the annual discount rate (assumed 10%/yr). The rotation period that maximizes discounted yield-per-recruit is 6 years (Fig. 2). If prices as a function of meat weight are known, it would also be possible to do a similar analysis to maximize discounted value-per-recruit.

Yield isopleths, commonly used to visualize yield-per-recruit analysis (Beverton and Holt, 1957), are given in Figure 3A (yield-per-recruit) and 3B (discounted yield-per-recruit). For rotational analyses, fishing mortality is placed on the x-axis and rotational period on the y-axis. Note again that for longer rotation times, the decline in yield for fishing mortalities greater than F_{MAX} is much less than without rotation. The value of F_{MAX} and maximum yield-per-recruit increases slightly with longer rotation periods.

Biomass-per-recruit for no rotation, 3-, 6- and 9-yr pulse rotation strategies is given in Figure 4. Compared to constant fishing, rotational fishing gives increased biomass-per-recruit; this increase is most evident for the longer

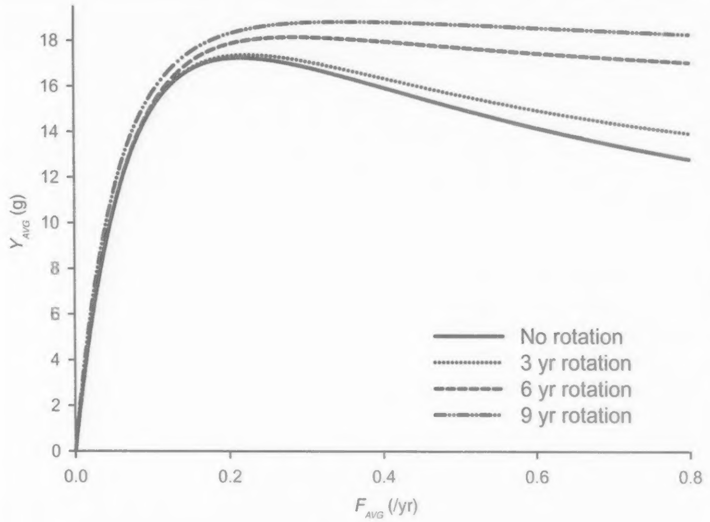

Figure 1

Yield-per-recruit curves for Georges Bank sea scallops with no rotation and with 3-, 6-, and 9-yr pulse rotations.

rotations and higher fishing mortalities. At F_{MAX}, the increase in biomass-per-recruit is slight, unless a very long (e.g. 9-yr) rotational period is employed.

The performance of rotation can be assessed as a function of selectivity at size. Figure 5A gives maximal yield-per-recruit for a number of pulse rotation strategies and a variety of values of h_{min}, the smallest size selected by the gear; the size of full selectivity, h_{full}, was taken as h_{min} + 23 mm (consistent with the assumed current gear selectivity pattern; see Table 1). Rotation can give substantial yield-per-recruit advantages when the gear selects animals of well below optimal size, especially for longer periods. However, long-period rotation actually gives less yield-per-recruit than constant fishing for larger values of h_{min}. Figure 5B gives a similar plot for biomass-per-recruit, where fully recruited fishing mortality is fixed at F = 0.3 in all cases. Unlike yield-per-recruit, rotational fishing increases biomass-per-recruit regardless of the selectivity pattern, especially when the rotational period is long.

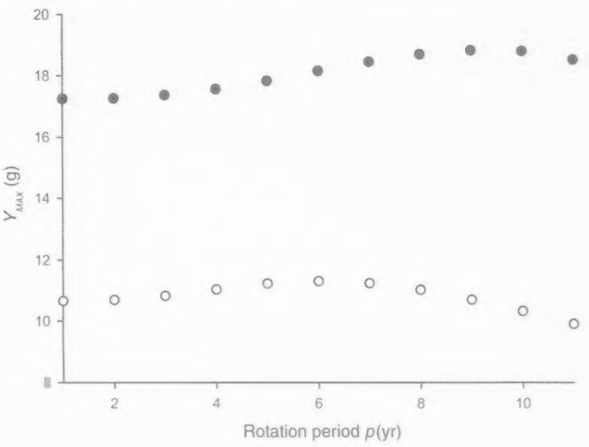

Figure 2

Maximum yield-per-recruit (solid circles) and discounted (10%) yield-per-recruit (open circles) for Georges Bank sea scallops with a pulse rotation of periods between 1 and 11 years.

Yield-per-recruit from different cohorts under a rotational system can vary considerably. The cohort which recruits into the fishery at about the time of the closure produces the highest yield-per-recruit, whereas the cohort that reaches exploitable size at about the time that the area is opened has the lowest. Figure 6 gives the mean yield-per-recruit together with that of the cohorts with the highest and lowest yield-per-recruit under six-year pulse rotational management (i.e. Y_{AVG}, $Y^{(1)}$, and $Y^{(6)}$, respectively). A 31% increase in maximal yield compared to constant fishing (and 25% increase over the average yield-per-recruit under rotation) can be obtained from the cohort whose yield-per-recruit is the highest under rotation. Note that, unlike conventional yield-per-recruit curves for sea scallops, yield-per-recruit from this cohort is almost completely insensitive to effort beyond a certain level.

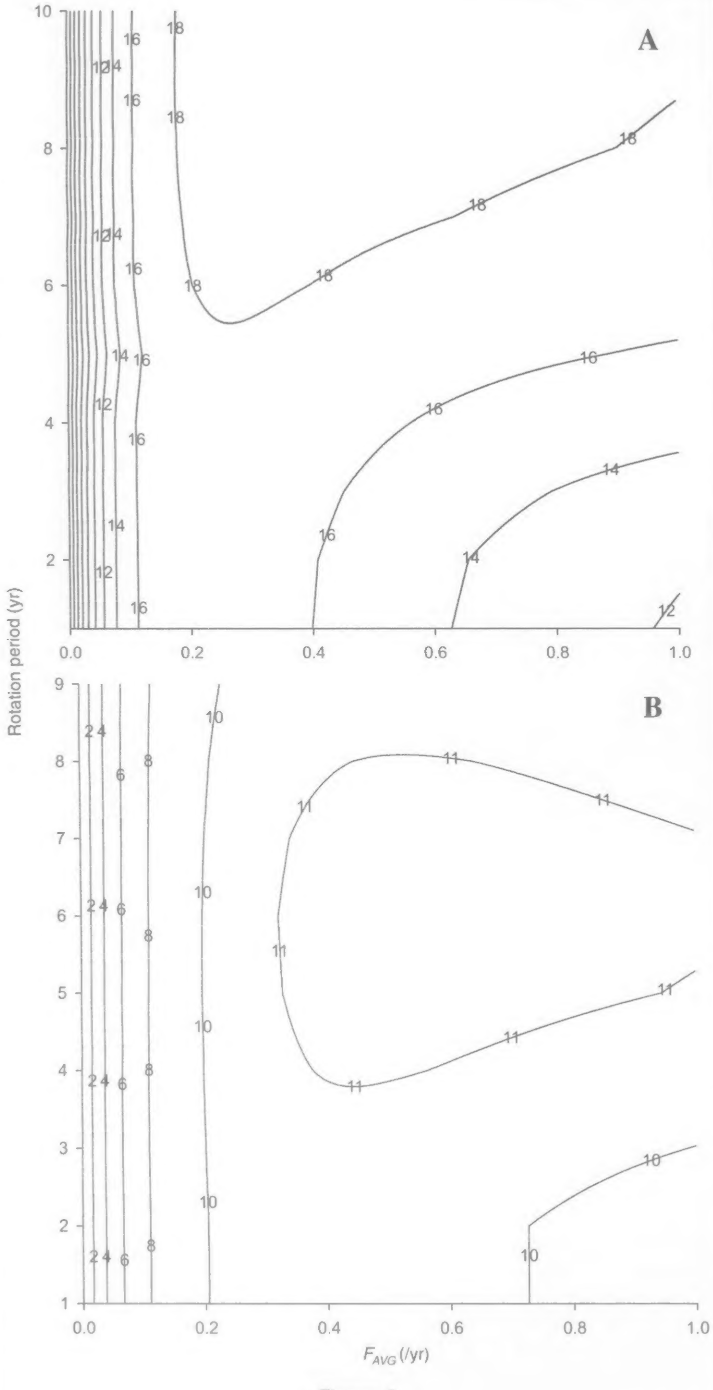

Figure 3

Yield-per-recruit (**A**) and discounted (10%) yield-per-recruit (**B**) isopleths for Georges Bank sea scallops with pulse rotation. Note that the *y* axes represent rotation period.

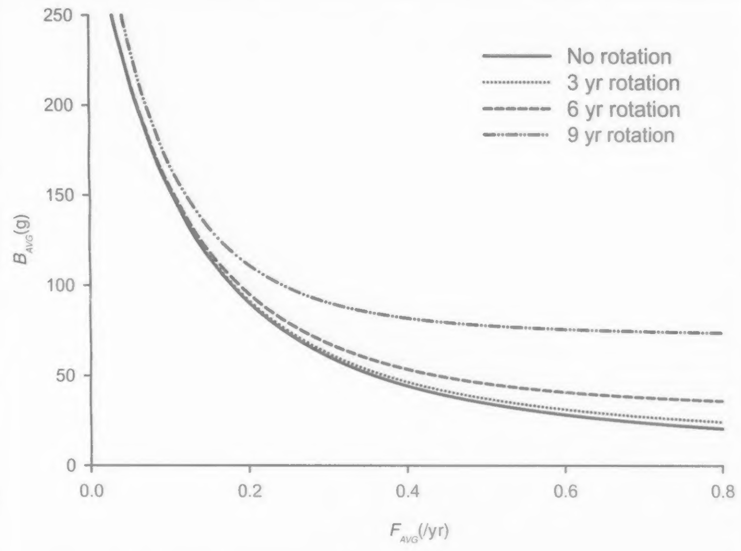

Figure 4

Biomass-per-recruit for Georges Bank sea scallops with no rotation and with 3-, 6-, and 9-yr pulse rotations.

Table 2

Calculated values of F_{MAX}, Y_{MAX}, B_{MAX}, and discounted (*Dsc*) Y_{MAX} (in grams, with a 10% discounting factor) for (**A**) pulse rotation with no incidental fishing mortality, (**B**) pulse rotation with 15% incidental fishing mortality, and (**C**) symmetric rotation with no incidental fishing mortality. p = period of rotation.

	p	F_{MAX}	Y_{MAX}	B_{MAX}	*Dsc* Y_{MAX}
A	1	0.217	17.25	84.0	10.66
	2	0.219	17.27	83.6	10.70
	3	0.225	17.38	82.4	10.83
	4	0.239	17.57	79.6	11.04
	5	0.259	17.84	76.8	11.24
	6	0.287	18.17	74.5	11.32
	7	0.324	18.47	73.8	11.25
	8	0.351	18.71	77.4	11.03
	9	0.363	18.84	84.2	10.71
	10	0.372	18.82	92.0	10.34
	11	0.374	18.69	100.6	9.93
B	1	0.192	14.62	91.9	8.79
	2	0.193	14.62	91.6	8.80
	3	0.197	14.68	90.5	8.88
B (cont.)	4	0.205	14.81	88.4	9.01
	5	0.219	14.99	85.4	9.16
	6	0.236	15.20	82.8	9.25
	7	0.257	15.43	81.2	9.25
	8	0.277	15.63	82.2	9.15
	9	0.292	15.75	86.0	8.96
	10	0.300	15.8	91.8	8.70
	11	0.302	15.75	99.0	8.4
C	2	0.219	17.27	83.6	10.70
	4	0.225	17.4	82.5	10.82
	6	0.235	17.56	81.0	10.90
	8	0.244	17.68	81.1	10.85
	10	0.248	17.73	83.5	10.68
	12	0.253	17.64	86.3	10.44

Yield-per-recruit curves for 6-yr symmetric rotation (i.e. closed for three years and then opened for three years), 10-yr symmetric rotation, 6-yr pulse rotation, and no rotation are given in Figure 7. Symmetric rotation gives yields-per-recruit that lie between that of pulse rotation and constant fishing. Maximum yield-per-recruit, together with the associated B_{MAX}, and maximal discounted yield for pulse rotation, with and without 15% incidental mortality, and for symmetric rotation without incidental mortality, are given for various rotation periods in Table 2.

Results from yield-per-recruit runs with incidental fishing mortality (Table 2B) show similar patterns to

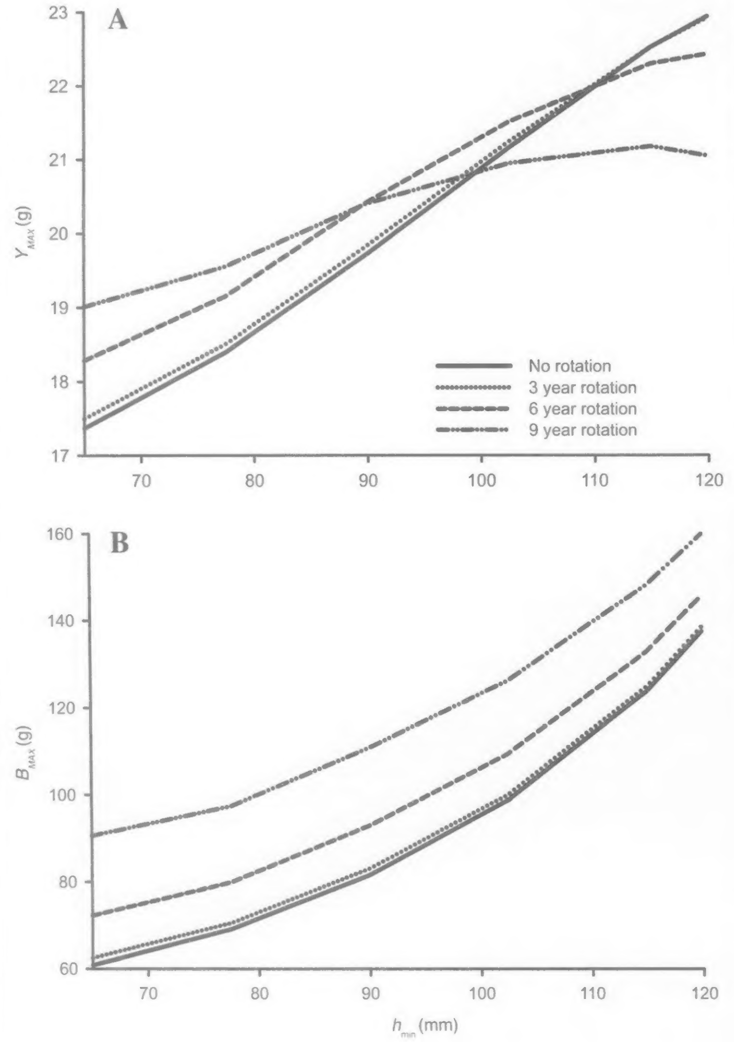

Figure 5

(**A**) Yield-per-recruit and (**B**) biomass-per-recruit for no rotation (solid line), 3-yr (dotted line), 6-yr (dashed line) and 9-yr (dot-dashed line) pulse rotations of sea scallops as a function of minimum selected shell height h_{min}. Scallops are assumed to be fully recruited to the fishery at shell height h_{min} + 23 mm.

results with no incidental fishing mortality (Table 2A). Note that both yields and the value of F_{MAX} are reduced if incidental fishing mortality exists and that the penalty for overfishing without rotation is somewhat higher (about 67% loss in yield-per-recruit for fishing at F=1 without rotation compared to 38% without incidental mortality). However, at F_{MAX}, the loss of yield due to incidental mortality is about the same for rotational fishing as for steady fishing.

Discussion

Rotational fishing can generate increased yield- and biomass-per-recruit for sea scallops compared to nonrotational fishing. The expected increase in maximum yield-per-recruit is modest (<10%) for a fixed rotational pattern. The over 30% gain in yield-per-recruit obtained from cohorts that reached exploitable size near the time of the closure is partially cancelled by the loss of yield-per-recruit

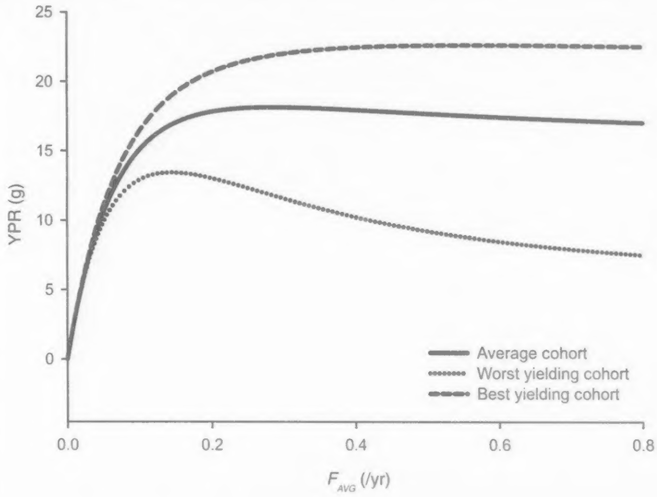

Figure 6

Yield-per-recruit for a 6-yr pulse rotation of Georges Bank sea scallops from an average cohort, and those that benefit the most and the least from rotation.

on those cohorts that reached exploitable size at about the time the area was reopened, thereby resulting in only a modest gain in yield-per-recruit. A more substantial gain in maximum yield-per-recruit (up to 30% greater than constant fishing) can be obtained if the closure is timed to optimally exploit an unusually large year class. These results are consistent with several studies that indicate that periodic fishing can often increase yields over constant fishing (Botsford, 1981; De Klerk and Gatto, 1981; McCallum, 1988; Clark, 1990; Myers et al., 2000).

A second, and perhaps more important, advantage of rotational fishing is that it alleviates the impact of both growth and recruitment overfishing. Growth overfishing (i.e. fishing at a level higher than F_{MAX}) under rotational management induces a substantially smaller reduction in yield-per-recruit than would occur with constant fishing. Rotation also increases biomass-per-recruit for sea scallops, especially for levels of F above F_{MAX}, thereby reducing the impact of possible recruitment overfishing. It might be argued that overfishing should not be occurring in any case. However, even when management measures are taken to eliminate overfishing, it can still occur, for example, if 1) reference points are incorrect because of uncertainty in life history parameters; 2) fishing mortality, or the effect of management measures on fishing mortality, has been underestimated; or 3) there is localized overfishing because of spatial variation in fishing intensities or life history parameters (or variation in both), even though when averaged spatially, $F_{AVG} \leq F_{MAX}$ (Caddy, 1975; Hart, 2001). Rotational fishing can thus be thought of as part of a precautionary strategy. In so much as it may increase maximum yield, rotational management is superior to many other precautionary measures that reduce yield. The only costs of rotational management are the costs of administrating and enforcing such a system, and socioeconomic costs from temporary closures of traditional fishing grounds. The latter might be significant if closures force fishermen to make long distance steams to unfamiliar areas. Because the optimal F_{AVG} under rotation is only slightly greater than the nonrotational F_{MAX}, the amount of effort and fleet capacity required to optimize yield-per-recruit under rotation is about the same as that needed under uniform fishing.

Rotation also imposes practical constraints on the level of average fishing effort, thereby limiting the extent to which stocks can be overfished. Fishing mortality rates for U.S. sea scallop stocks were estimated as exceeding 1.0/yr during the late 1980s and early 1990s.[1] This would correspond under a 6-yr pulse rotation to an unaveraged fishing mortality of over $F = 6$ in the area open to fishing. Such a high fishing morality rate, corresponding to about a 98% exploitation rate for fully recruited scallops, is likely to be impractical for both physical and economic reasons. Thus, F_{AVG} in a rotation plan would likely be considerably below the high levels seen in the late 80s and early 90s, even if there was no other restriction on fishing effort other than pulse rotation.

Myers et al. (2000) claimed that "near-optimal yields are achieved across a wide range of fishing mortalities" in their rotational scheme. However, much of their analysis was confounded by their use of unaveraged open area fishing mortality ($=pF_{AVG}$) on the x axis of their per-recruit curves. For example, in the case analyzed in Myers et al (2000), where one of p areas would be fished each year, the fishing mortality F applied in the area open to fishing in a 9-yr rotation (i.e. 1/9 of the area would be fished each

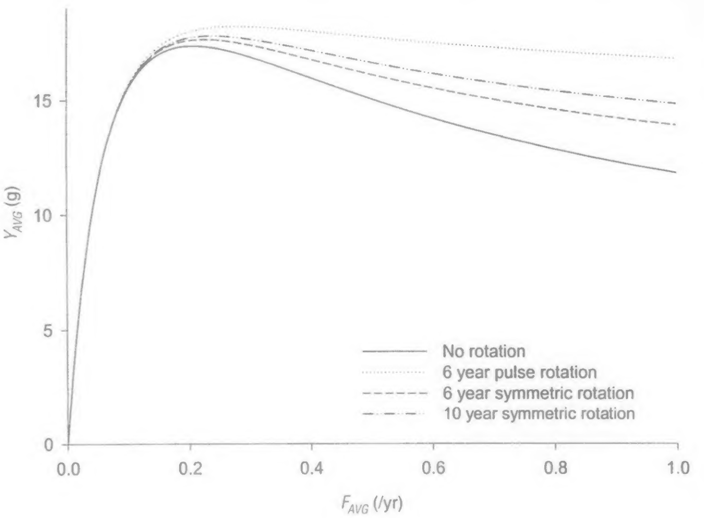

Figure 7

Comparison of yield-per-recruit for Georges Bank sea scallops with 6-year and 10-year symmetric rotations with that of a 6-yr pulse rotation or no rotation.

year and that $F = F_{AVG}/9$) would represent one ninth of the actual effort as the same F applied to the whole area under non-rotational fishing. Use of unaveraged fishing mortality has the effect of stretching the x axis by a factor of p, thereby making their graphs appear flatter than they actually are. F_{AVG} is representative of not only the true time-averaged fishing mortality but also in many cases would be proportional to spatially averaged fishing effort (as measured by, e.g., hours fished).

Myers et al. (2000) also suggested that rotational fishing would help lessen the impact of indirect (incidental) fishing mortality on yield-per-recruit. The analysis given in the present study indicates that incidental mortality lowers yield-per-recruit at F_{MAX} about the same amount regardless of whether or not rotational fishing is employed. At levels of fishing mortality well above F_{MAX}, rotational fishing does appear to modestly decrease the loss of yield-per-recruit due to incidental mortality. This decrease is due to the fact that incidental mortality, by somewhat lowering F_{MAX}, exacerbates the effects of overfishing, whereas rotation alleviates the loss of yield-per-recruit due to overfishing.

The effectiveness of sea scallop rotational fishing can be understood by examining fishing mortality at size for various rotational strategies. Figure 7 shows fishing mortality as a function of shell height for no rotation and for 3-, 6-, and 9-yr rotations for $F_{AVG} = 0.2$ (Fig. 8A), and $F_{AVG} = 0.6$ (Fig. 8B). Rotational fishing (especially for longer periods) tends to reduce the fishing mortality on small scallops and shift this effort onto larger individuals, thereby increasing yield-per-recruit, especially when overfishing is occurring. The periodic peaks in fishing mortality seen in the rotational strategies occur at the sizes where a new cohort begins to be fished (i.e. when the scallops are some integer number of years past their age at 40 mm). In practice, these peaks are likely to be much less pronounced because of variations in individual growth rates and settlement times. However, the qualitative pattern of increasing selectivity with size should not be affected by such variations.

Sea scallops are an ideal candidate for rotational management, combining fast growth and low natural mortality with a sedentary adult lifestyle. In addition, sea scallops are recruited into the fishery at a size that is well below optimal from a yield-per-recruit perspective. The increase in size-selectivity induced by rotation described above should therefore induce an increase in yield-per-recruit. However, in those fisheries where the size-at-entry to the fishery is much larger, rotation would not be expected to induce gains in maximal yield-per-recruit (see Fig. 5A). On the other hand, it appears that rotation increases biomass-per-recruit regardless of the size-selectivity of the fishery (Fig. 5B). Botsford et al. (1993) found that rotation increased biomass- but not yield-per-recruit for red sea urchins. These results are consistent with the above discussion because the minimum legal size for landing the urchins was already near-optimal.

Although the exact levels of yield- and biomass-per-recruit obtained with or without rotation are sensitive to such factors as natural mortality and growth rates, the relative gains of rotation over constant fishing are much less sensitive to these factors. Rotation will improve yield-per-recruit under a broad range of parameter choices provided that 1) the ratio of growth to mortality K/M is

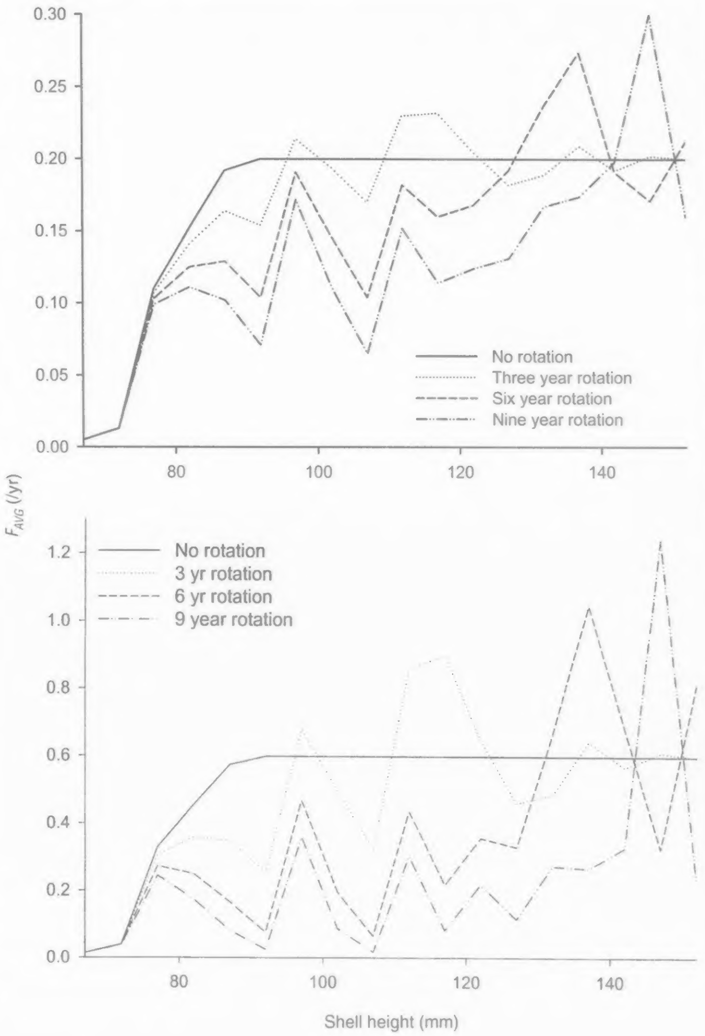

Figure 8

Mean fishing mortality at length for Georges Bank sea scallops with no rotation and with 3-, 6-, and 9-yr pulse rotations for (**A**) $F = 0.2$, and (**B**) $F = 0.6$.

sufficiently high (greater than about 0.5 with the other parameters in the model fixed as given in Table 1), and 2) size-selectivity is suboptimal. Rotation improves biomass-per-recruit under even a wider range of parameters.

Allee effects may occur in broadcast spawners such as urchins and scallops. Areas that are closed for several years may allow these animals to form dense aggregations (that would likely be heavily fished if not closed), thereby improving fertilization success (Botsford et al., 1993). Such an effect would mean that rotation could produce greater benefits in fecundity than would be suggested by biomass- or eggs-per-recruit curves.

Metapopulation structure might also be considered when designing a rotational strategy. If recruitment is limited by the supply of settling larva, an area that is a source of larva might be fished less than that required to maximize yield-per-recruit in order to increase larval supply (Tuck and Possingham, 1994).

The calculations that indicate long optimal rotational periods assume low constant natural mortality, independent of age or density, based on the study of Merrill and Posgay (1964). There is some evidence that the natural mortality rate of sea scallops may increase with age or size for shell heights greater than about 110 mm (Mac-

Donald and Thompson, 1986). If this is the case, optimal rotational periods would be shorter than calculated here, although the yield-per-recruit formalism would remain valid. More serious problems would be caused if there is density-dependent mortality of adults or if high adult densities inhibited recruitment because rotational closures can induce higher densities than would constant fishing. If either of these processes occur, shorter rotation periods would be advisable to minimize this problem. For sea scallops, however, observations of areas that have been closed to fishing for a number of years give no indication that such density-dependent processes are occurring (Fig. 2b in Hart 2001, and Table B5-8 in NEFSC[1]).

An extreme case of rotational fishing is true pulse fishing, where all exploitable individuals are removed at periodic intervals (see e.g. Sluczanowski, 1984). Thus, true pulse fishing corresponds to pulse rotation (as defined in the present study) with an infinite fishing mortality. Such pulse fishing is not optimal for sea scallops, as can be seen by the slight decline of yield-per-recruit at high fishing mortalities in Figure 1 because at very high fishing mortalities, the partial selectivity of the gear loses its effectiveness and all individuals that are even slightly selected to the gear (i.e. that are even slightly greater than $h_{\min}$) will be removed. To put it another way, at high fishing mortality rates, the additional (i.e. marginal) catch obtained from a further increase in F will disproportionately consist of small animals, thereby reducing yield-per-recruit. Pulse fishing would be optimal if knife-edge selectivity is assumed. For this reason, the assumption of knife-edge selectivity would lead to unrealistic results for cases such as sea scallops, where gear selectivity increases more gradually with size. Proper application of rotational theory therefore requires a careful examination of fishing selectivity with size.

Pulse fishing can be related to the classic Faustmann theory of forest rotation (see e.g. Reed, 1986; Clark, 1990). In this theory, if a stand of trees in an area that has last been harvested t years previously has value $V(t)$, then the optimal time to harvest the trees satisfies

$$V'(t) = \delta\big(V(t) - c\big) + \delta \frac{V(t) - c}{\exp(\delta t) - 1}, \tag{6}$$

where δ = the discount rate; and
c = the cost of harvesting.

In the case of a fishery, $V(t)$ would represent the expected value of the exploitable stock (e.g. those of shell height greater than $h_{\min}$) at time t. (Note that in this context, unlike the original forest application, it is not necessary to assume that all exploitable individuals are the same age.) In the case of scallops, assuming all scallops command the same price per unit weight, $c = 0$, and $\delta = 0.1$, this formula would give an optimal rotation period of about 6.1 years (the optimal period would be moderately longer for realistic positive values of c). This value corresponds well to the rotation time of 6 years that optimizes discounted yield-per-recruit (see Fig. 2). However, the yield-per-recruit for 6-yr pulse fishing, $V(6)$, is less than 80% of the maximal yield-per-recruit obtained by fishing uniformly. Again, the reduced yield-per-recruit is due to the fact that pulse fishing induces knife-edge selectivity at $h_{\min}$, rather than the usual gradual increase in vulnerability to the gear.

Symmetric rotational strategies appear to give less benefit than does pulse rotation. However, optimal pulse rotation would require high, and possibly impractical, levels of effort in an area when it is opened (e.g. F of about 1.7 for a 6-yr pulse rotation). In addition, such a strategy would require that areas be closed most of the time, possibly inducing social-economic disruptions by closing traditional fishing grounds for long periods. Compared to pulse rotation, symmetric rotation requires less concentrated effort, allows areas to be open half the time, and is less sensitive to the assumption of constant natural mortality. One possible compromise between pulse and symmetric rotation is to close an area for half the time and then gradually increase effort during the opening. For example, an area might be closed for three years and then fished for the next three years at F_{MAX}, $2F_{\mathrm{MAX}}$, and $3F_{\mathrm{MAX}}$, respectively.

Questions have been raised regarding the appropriateness of the use of whole-stock fishing mortalities as targets or reference points for fisheries of sedentary stocks that include rotational or long-term closures (or both) (NEFSC[2]). The solid line in Figure 9 gives the whole stock (biomass-weighted) fishing mortality (assuming constant recruitment everywhere) for a pulse rotational system consisting of six areas, one of which is fished each year in turn. This whole-stock fishing mortality was obtained by simply dividing the yield-per-recruit for a 6-yr pulse rotation by the corresponding biomass-per-recruit. The x axis is F_{AVG}, which should be proportional to true effort. As can be seen, whole-stock fishing mortality is proportional to effort for low fishing mortalities, but then flattens to a maximum of just under 0.4.

A similar situation can happen even if an area is fished uniformly, except that a portion of the area is set aside as an indefinite closure. The dashed line in Figure 9 gives an example for the case when 10% of the area is permanently closed and is allowed to equilibrate to the biomass-per-recruit corresponding to zero fishing mortality. Whole-stock fishing mortality shows a relationship to the actual fishing effort (the fishing effort in the open area only) in the open areas that is similar to that of rotational fishing. In both cases, closed area biomass dominates the whole-stock fishing mortality calculation at high fishing effort. The yield at high fishing effort is essentially derived from incoming recruitment, which is not sensitive to fishing effort for very high effort levels. Therefore, the whole-stock fishing mortality becomes nearly constant when effort is high.

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[2] NEFSC (Northeast Fisheries Science Center). 1999. Report of the 29th northeast regional stock assessment workshop (29th SAW). Stock Assessment Review Committee (SARC) consensus summary of assessments. NEFSC Ref. Doc. 99-14, 347 p. [Available from NEFSC, 166 Water St., Woods Hole, MA 02543.]

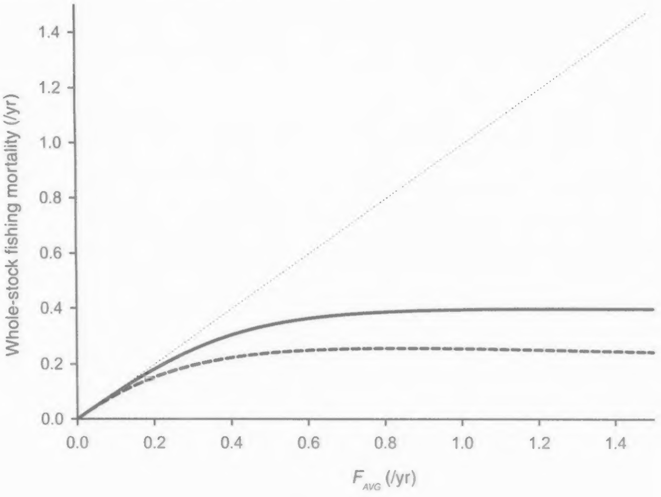

Figure 9

Whole-stock fishing mortality as a function of effort (F_{AVG}) for sea scallops with a 6-yr pulse rotation (solid line), and constant fishing with 10% of the area permanently closed (dashed line). The dotted line is the line $y = x$.

The current situation for sea scallops in Georges Bank gives an even more extreme example of this phenomenon. About 80% of the biomass lies in the groundfish areas that have been closed to scallop fishing for most of the time since December 1994. Because these areas will be closed to scalloping in 2002, the whole-stock fishing mortality in this year cannot exceed the F_{MAX} reference point of 0.24. Therefore, according to the current overfishing definition (the whole-stock F is below F_{MAX}), the stock cannot be overfished. Nonetheless, the fishing mortality in the open areas may exceed F_{MAX}, resulting in growth overfishing in these areas. Thus, the stock in the open areas could be overfished from a yield-per-recruit perspective even if the whole-stock F is below F_{MAX}.

The opposite situation could also occur. If scallops in the groundfish closed areas on Georges Bank were fished more than slightly above the $F_{MAX} = 0.24$ reference point, the whole-stock fishing mortality would also be above this reference point and overfishing would be considered to be occurring. However, an area that has been closed for a number of years should be fished harder, compared to an area that has never been closed, once the area is reopened in order to maximize yield-per-recruit. Thus, a strategy that would maximize yield-per-recruit might require a whole-stock F that would in some years be higher, and in some years lower, than the conventional overfishing reference point.

A whole-stock fishing mortality rate may therefore not be the most appropriate metric for overfishing definitions when some areas are temporarily or permanently closed to fishing. Its value may not be representative of the yield-per-recruit that could be obtained at that level of fishing mortality. Furthermore, when most of the biomass is in closed areas, estimated whole-stock fishing mortality may be more sensitive to variations in recruitment and measurement error than to actual changes in effort.

As an alternative to a whole-stock fishing mortality metric, the following considerations are suggested for a fishing effort measure that is compatible with yield-per-recruit calculations. (1) Stock from areas that are not fished in a given time period should not be included in the fishing mortality calculation for that time period. In a relatively sedentary stock, the amount of biomass in the closed areas is irrelevant in determining the yield-per-recruit that will be obtained from the stock in the open areas. (2) Time-averaging of fishing mortality in the open areas is required to take into account the previous fishing history of the area. An area that has been closed for a number of years needs to be fished harder once opened than an area that has been continuously fished in order to maximize yield-per-recruit.

Based on these considerations, the time-averaged fishing mortality computed from the open areas only, F_{AVG}, is an appropriate measure of fishing mortality in fisheries managed by using rotational or indefinite closures. It is natural to take the averaging period equal to the rotational period p. With this metric, F_{MAX} is only slightly sensitive to the rotational period p and completely insensitive to the level of closed area biomass. Indeed, even if no closures existed, but fishing effort varied with time, it may still be advisable to employ a time-averaged fishing mortality because the previous history of fishing mortalities strongly affects the level of effort required to maximize future yield-per-recruit. If an area has been fished harder than F_{MAX} for a number of years, so that the population size-structure in this area is smaller than the equilibrium size-structure obtained by fishing at F_{MAX}, then fishing the next year at a level somewhat below F_{MAX} will improve long term yield-per-recruit. Similarly, if an area has been fished below F_{MAX}, so that its size structure is larger than what would occur when fishing at a constant rate of F_{MAX}, then it may be optimal to temporarily fish at a level higher than F_{MAX}.

In summary, rotational fishing can improve yield- and biomass-per-recruit for long-lived sedentary stocks such as sea scallops. Rotational management can be part of a precautionary strategy because it can help alleviate the effects of growth and recruitment overfishing. Rotational management will however require a rethinking of conventional yield-per-recruit reference points.

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Appendix

Basic yield-per-recruit model

This appendix describes the basic yield-per-recruit model used for a cohort. In this model, recruits start at a specified shell height (or length) h_0. The shell height is converted into a starting age a_0 by using a von Bertalanffy growth equation. The shell height at time t is also obtained by using the von Bertalanffy growth curve. The shell height is converted into a meat weight by using a shell-height/meat weight formula:

$$w = \exp(a + b\ln(h)), \tag{7}$$

where w and h are in units of grams and millimeters, respectively.

Natural mortality occurs at a rate M, assumed for these simulations to be constant for all ages (M=0.1). The fishing mortality rate $F(h)$ on a scallop of shell height h is given by $F(h) = F_0J(h)$, where F_0 is the fully recruited fishing mortality rate and $J(h)$ is the selectivity of the gear. $J(h)$ was taken to be 0 if h is less than a minimum shell height h_{min}, 1 if h is greater than a fully recruited threshold size h_{full}, and interpolated linearly as

$$J(h) = \frac{h - h_{\min}}{H_{\text{full}} - h_{\min}} \tag{8}$$

if $h_{\min} < h < h_{\text{full}}$. Individuals that are caught by the gear but are smaller than a maximum cull size h_d, are discarded and are subject to a discard mortality d. In these simulations, d is taken to be 0.2 (DuPaul[3]); however, the results are not very sensitive to the exact value of this parameter. All individuals caught at a size greater than h_d are assumed to be landed and are included in the total yield. $F_c(h)$ denotes the rate at which scallops of shell height h are caught and retained (i.e. not discarded).

The possibility has been raised that some scallops may be killed but not captured by the gear (Caddy, 1973; Myers et al. 2000). Caddy (1973) estimated that 15–20% of the scallops remaining on the bottom in the path of a scallop dredge are killed but not captured by the dredge. Murawski and Serchuk[4] estimated that less than 5% of the scallops remaining in the path of the dredge suffered incidental (noncatch) mortality. In order to use the above studies to estimate the relationship between incidental fishing mortality F_I and the fully recruited capture fishing mortality rate F_0, it is necessary to know the efficiency e of the dredge on a fully recruited individual. Denote by i the fraction of scallops that suffer mortality among those that were in the path of the dredge but that were not caught, so that i is estimated at 0.15–0.2 by Caddy (1973), and less than 0.05 by Murawski and Serchuk.[3] The ratio R of fully recruited scallops in the path of the dredge that are caught to those killed but not caught is

$$R = e / [i(1-e)]. \tag{9}$$

If fully recruited scallops suffer capture fishing mortality at rate F_0, then the rate of incidental fishing mortality will be

$$F_I = F_0 \,/\, R = F_0 i\,(1 - e)/e. \tag{10}$$

If e is taken as 50% (estimated as the average scallop dredge efficiency on Georges Bank[5]), then F_I would be in the range 0.15 F_0 to 0.2 F_0 according to Caddy (1973) and less than 0.05 F_0 according to Murawski and Serchuk.[3] To ascertain the effects of incidental fishing mortality on the yield-per-recruit calculations, model runs were performed with no incidental mortality, and also when $F_I = 0.15\,F_0$; incidental fishing morality was applied to all size groups.

Let $Z(h)$ be the total mortality rate at shell height h (i.e. the sum of natural mortality, and discard, indirect, and landed fishing mortality). Then the fraction of recruits remaining t years after the beginning of the simulation is

$$S(t) = \exp\left(-\int_{a_0}^{t} Z(\tau)d\tau\right). \tag{11}$$

Total yield- and biomass-per-recruit are calculated by the formulas:

$$Y = \int_{a_0}^{a_f} S(t)F_c(h(t))w(h(t))dt \tag{12}$$

$$B = \int_{a_0}^{a_f} S(t)w(h(t))dt, \tag{13}$$

where a_f = the ending age of the simulation, taken to be $30 + a_0$.

For convenience in these simulations, a_0 is taken to be 2 years; this age is assumed to correspond to a shell height of precisely 40 mm. In the rotational simulations reported in this study, the fully recruited landed fishing mortalities $F_c(h)$ ($h>h_{\text{full}}$) are assumed to vary periodically and are given in year k by F_{j+k}, where j is the year that the cohort reaches the starting age a_0.

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Estimating long-term growth-rate changes of southern bluefin tuna (*Thunnus maccoyii*) from two periods of tag-return data

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Abstract—Southern bluefin tuna (SBT) (*Thunnus maccoyii*) growth rates are estimated from tag-return data associated with two time periods, the 1960s and 1980s. The traditional von Bertalanffy growth model (VBG) and a two-phase VBG model were fitted to the data by maximum likelihood. The traditional VBG model did not provide an adequate representation of growth in SBT, and the two-phase VBG yielded a significantly better fit. The results indicated that significant change occurs in the pattern of growth in relation to a VBG curve during the juvenile stages of the SBT life cycle, which may be related to the transition from a tightly schooling fish that spends substantial time in near and surface shore waters to one that is found primarily in more offshore and deeper waters. The results suggest that more complex growth models should be considered for other tunas and for other species that show a marked change in habitat use with age. The likelihood surface for the two-phase VBG model was found to be bimodal and some implications of this are investigated.

Significant and substantial differences were found in the growth for fish spawned in the 1960s and in the 1980s, such that after age four there is a difference of about one year in the expected age of a fish of similar length which persists over the size range for which meaningful recapture data are available. This difference may be a density-dependent response as a consequence of the marked reduction in the SBT population. Given the key role that estimates of growth have in most stock assessments, the results indicate that there is a need both for the regular monitoring of growth rates and for provisions for changes in growth over time (possibly related to changes in abundance) in the stock assessment models used for SBT and other species.

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Estimating growth rates has been a major focus of fisheries research throughout the twentieth century, and a large body of literature exists on the topic (e.g. Lee, 1912; Ford, 1933; Walford, 1946; Manzer and Taylor, 1947; Allen, 1966; Yukinawa, 1970; Pitcher and MacDonald, 1973; Kimura, 1980; Fournier et al., 1990). This literature reflects, at least in part, the fundamental importance of information on growth rates in stock assessments and the subsequent provision of management advice for commercially harvested fish populations. For example, growth information is required for yield-per-recruit analyses and for the estimation of spawning stock biomass in the estimation of stock-recruitment relationships. In addition, for a number of species, estimates of growth rates have been the primary or only source of information that can be used to estimate the age of individual fish and the age distribution of commercial catches (particularly for tropical species and for tunas and billfish). Such information on age is a critical component required in the analyses and models used to assess and manage these fish stocks (Bayliff, 1991; Clay, 1991; Caton, 1991; Wild, 1994; Wild and Hampton, 1994; Polacheck et al.[1]).

Almost all the work on modeling growth has centered on modeling growth rate as a continuous, smooth, monotonically decreasing function of age, and the von Bertalanffy (1938) growth (VBG) equation, and its extensions, have been the most common approach used. In addition, the growth process has frequently been modeled as static. Temporal variations in average growth for fish of the same size, or age, (due, for example, to changes in the physical environment or population density) are often ignored or considered to be relatively minor (with some notable exceptions—e.g. Le Cren, 1958; Southward, 1967; de Veen, 1976; Toresen, 1990; Ross and Nelson, 1992; Kaeriyama, 1996; Sinclair and Swain, 1996).

For the large pelagic tunas and billfishes, the von Bertalanffy growth equation and extensions has been the standard used for modeling growth (Bayliff, 1980). For a variety of tuna species, numerous growth studies have been conducted, and generally a reasonable range of parameter values has been estimated (e.g. see the sets of parameter values estimates for the eight scrombrid species in Bayliff, 1980).

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[1] Polacheck, T., A. Preece, A. Betlehem, and N. Klaer. 1998. Treatment of data and model uncertainties in the assessment of southern bluefin tuna stocks. *In* Fishery stock assessment models (F. Funk et al., eds.), p. 613–637. Alaska Sea Grant College Program Report AK-SG-98-01. Univ. Alaska, P.O. Box 755040, Fairbanks, AK 99775-5040.

Bayliff (1988) also investigated regional growth differences in Pacific skipjack and yellowfin tunas. Interpretation as to whether any differences found are merely an artifact of the data collection or procedures used or whether they reflect real temporal or spatial difference has generally not been possible because the basic data (e.g. tagging, hard parts, length-frequency data), data collection procedures, analytic approaches, and the areas and time periods from which the data were collected have varied greatly among studies.

For southern bluefin tuna (SBT) (*Thunnus maccoyii*), extensive juvenile tagging programs were conducted in the 1960s and 1980s, and a large number of returns with measured lengths were recovered. From both periods, some returns were received after times at liberty in excess of 10 years. These two sets of tagging experiments provide the basis for the direct comparison of growth over a time span of 30 years. Also, because of the large number of tags returned in these studies, a more detailed examination of the adequacy of the von Bertalanffy growth equation as a model of the growth process is possible than with many data sets. These tagging data (primarily those from the 1960s) have been used as a basis for a number of analyses of growth rates (Murphy, 1977; Kirkwood, 1983; Hearn, 1986; Hampton, 1991; Lucas[2]). In the present paper, we present results of the analyses of the growth increment data from these two sets of tagging experiments. We examine these data both in terms of 1) whether SBT growth differed between the tagging periods and 2) whether there was a change in the growth process between adult and juvenile SBT (i.e. whether a more complex model than the simple von Bertalanffy equation is required to provide an adequate description of SBT growth).

The results presented here incorporate and build upon the already cited published analyses of these tag-return data, unpublished reports, and discussions of SBT growth in scientific meetings on SBT (e.g. Hearn and Hampton[3]; Hearn and Polacheck[4]; Anonymous[5]).

Background: the SBT stock and fishery

SBT is a highly-migratory species that begins to spawn at about 10–12 years of age in waters south of Java during the southern summer, mainly from September to April (Farley and Davis, 1998). During the first year of life they tend to be transported south by the tropical Leeuwin Current to inshore waters between Perth and Esperance, Western Australia. From ages 1 to 4 years, they appear to mainly inhabit, at least in the summer months, the waters off the Great Australian Bight, southern New South Wales (NSW) and eastern Tasmania. Many move to oceanic waters during the winter months and apparently progressively so as they age. By five years of age almost all have migrated to oceanic waters between 30° and 50°S at all longitudes, but mostly in the Eastern Hemisphere.

Substantial surface fisheries operated off the south coast of Western Australia from 1969 to the mid 1980s, off the south coast of NSW from 1963 to the early 1980s, and off South Australia from 1964 to the present. Since 1959 a major Japanese longline fishery has operated in oceanic waters between 30° and 50°S, mainly from the mid-Atlantic and westwards to a few degrees west of New Zealand.

Materials and methods

Tagging programs

Description Large numbers of tagged fish were released by CSIRO staff in the period from 1959 to 1968 and again in the period from 1980 to 1984. The releases from these two periods are used in our present study. Most of the tagged fish were initially caught with pole-and-line gear with barbless hooks, although a relatively small number were caught with troll lines. After a fish was hooked, it was hauled aboard the vessel and placed on a measuring board (in the 1960s) or a vinyl cradle (in the 1980s), and its nose to caudal fork length was measured. The fish was then tagged by an operator who inserted a 12-cm plastic spaghetti dart tag into the fish about 4 cm to the rear of the second dorsal fin on either side of the fish and rereleased it into the water within about 30 seconds. After 1963 almost all fish were double tagged. The tag numbers and length of each fish were recorded, together with location and date of release. This information was later transferred to a computer database.

Tagging operations in both the 1960s and 1980s were concentrated in the nearshore, surface-water fisheries bordering the central and western southern coast of Australia and the southern coast of NSW. In the 1980s no tags were released from the NSW coast area because this component of the fishery had collapsed, and surface schools of juvenile SBT could no longer be found (Caton, 1991). The South Australian tagging took place in the Great Australian Bight or in the adjacent shelf waters generally between longitudes 128° and 136°E. Releases in Western Australia occurred in the Albany (between longitudes 112° and 119°E) and Esperance (between longitudes 119° and 125°E) areas. There were 33,309 juvenile SBT tagged by

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[2] Lucas, C. 1974. Working paper on southern bluefin tuna population dynamics ICCAT (Intenational Commission for the Conservation of Atlantic Tunas), SCRS/74/4. Collective Volume of Scientific Papers, vol. 111, p. 110–124. [Available from CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia.]

[3] Hearn, W. S. and J. Hampton. 1990. SBT growth change. Ninth trilateral meeting on SBT, Hobart, Australia, September 1990, SBFWS/90/8, 19 p. [Available from CSIRO and the Commission for Conservation of Southern Bluefin Tuna, P.O. Box 37, Deakin West, ACT 2600, Australia.]

[4] Hearn, W. S., and T. Polacheck. 1993. Estimating SBT age-at-length relations for the 1960s and 1980/90s. Twelfth trilateral meeting on SBT, Hobart, Australia, October 1993. SBFWS/93/4, 21 p. [Available from CSIRO and the Commission for Conservation of Southern Bluefin Tuna, P.O. Box 37, Deakin West, ACT 2600, Australia.]

[5] Anonymous. 1994. Report of the southern bluefin tuna trilateral workshop; Hobart, Australia, January/February 1994, 161 p. [Available from CSIRO and the Commission for the Conservation of Southern Bluefin Tuna, P.O. Box 37, Deakin West, ACT 2600, Australia.]

CSIRO personnel during the 1960s (1959 to 1968) and 10,743 during the early 1980s (1980 to 1984). Of these fish, 1972 and 4280, respectively, were later recaptured.

On recapture, fishermen recovered the tags and recorded the fish's length (if measured), location, and date. The tags with the recorded information were returned to the scientific staff at CSIRO, who then provided a reward. Most of the recapture lengths were measured by fishermen or factory staff, but about 31% were measured by scientists. Those measured by scientists cannot be considered a representative sample. In particular, all of the measurements for longer-term recaptured fish come from fishermen aboard Japanese longline vessels. In addition to length, longliners often reported the dressed weight and sometimes the whole weight, or both, of recaptured fish. In the 1960s Australian fishermen seldom reported any weight measurements, but in the 1980s they commonly reported the whole weight of recaptured fish.

Data selection The tagging experiments were conducted mainly within a narrow range of months at each site; therefore returns within a few months would be most strongly influenced by the seasonal differences found in SBT growth (Hearn, 1986; Burgess et al., 1991; Leigh and Hearn 2000). A nine-month period at liberty coincides with a low frequency in the times at liberty for the experiments; therefore we excluded data from analyses with less than 270 days at liberty. We also excluded data for which fish were tagged by fishermen, or when the recovery length, year, or month were reported by the tag finder to be unknown or uncertain.

Previously reported weight-length relationships (Warashina and Hisada, 1970; Hampton, 1986; Robins[6]) were used to identify and screen out dubious recapture data. The details of the screening procedures are documented by Hearn[7] and Anonymous.[5] Longline recaptures were excluded if the expected weight of a recaptured fish for its reported length was either less than 2/3 of the reported weight or greater than 1.5 times the reported weight. Some of the major inconsistencies were thought to be due to measuring the length of a fish without its tail or without its head (Lucas[2]). For surface fish in the 1980s, a high proportion of the weight-length data for recaptured fish from four vessels was inconsistent with the weight-length relationships noted above. All tag-return data from these four vessels were excluded. Another 2.5% of the 1980 data were excluded because of highly unlikely values for the ratio of the reported weight to length of the recaptured fish.

For the screening methods used, no assumption was made about the underlying growth curve, and these methods were designed so that they would not induce a bias into the results. The selection process yielded data sets that were sufficiently large for valid analyses, being 730 and 1450 for the 1960s and 1980s data sets, respectively. Note that for other tuna species the selection process used in our study (particularly the deletion of recaptured fish with short times-at-liberty) may cause problems because of smaller data sets (e.g. skipjack and yellowfin tunas in Bayliff, 1988).

Experimental assumptions The use of the tag-return increment data for estimating growth rates requires the following assumptions about the tagging protocols and data collection procedures:

1. Tagging does not retard growth.
2. The tagged fish are uniquely and correctly recorded at release and recapture.
3. The lengths of fish are measured without bias at release and recapture.
4. A wide range of fish sizes are represented, in recaptures at least.
5. There are no significant size-selection processes for fish within similar age ranges.

With respect to tagging effects, Hampton (1986) and Hearn (1986) have shown that there can be a significant weight loss of 7–12% for tagged fish in the first month after release. However, tagged fish recover this weight loss within a year at liberty, and there is no apparent difference between tagged and untagged fish after this time (Hearn, 1986). (There is little information available on weight loss of tagged fish at liberty between one month and one year.) In terms of length, Hearn and Hampton[3] could not detect a reduction of growth from growth increment residuals in the tag-return data even within the first 30 days after release. Limited data from the effect of handling and tagging fish in commercial farm pens indicated no retardation in growth in length after 150 days. These farm fish did show a loss in weight when first caged, but the weight was regained over a period of a few months (Anonymous[5]); therefore we do not think that tagging had any substantial effect on the growth rate of tagged fished in our study. With respect to the other assumptions, all fish were tagged with uniquely numbered tags. During tagging operations, tags were arranged in blocks of sequential numbers to avoid confusion and the misrecording of tag numbers. Return of the physical tag was required for fishermen to obtain the reward, and the double tagging of almost all fish since 1963 has allowed cross verification of tagging numbers, which allows little scope for error in the recording of tag numbers. Approximately 23% of the length measurements for the selected recaptured fish were measured by scientists. Mainly due to the deletion of short-term recaptured fish (i.e. < 270 days), this is less than that for all data (31%). For the fishermen-measured lengths, there was no reason to suspect any consistent bias, and comparison of the residuals for fishermen- and scientist-measured returns in the fitted models below did not indicate any systematic pattern. The recaptured fish used in our study ranged in size from 60 to 175 cm, although the number of fish in the larger size ranges was relatively small—less than 2% were larger than 140 cm. (The consequences of the small number of fish in the large-size category are discussed below.) Within both the surface and longline fishery, a range of sizes and age classes is harvested within a single operation. No indication exists that within the size range encompassed by a cohort at a given age, there existed significant gear or fishery size selectivity. Overall, the above basic assumptions seem reasonable in modeling growth from these SBT tagging data.

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[6] Robins, J. P. 1963. Synopsis of biological data on southern bluefin tuna, *Thunnus thynnus maccoyii* (Castlenau) 1872. FAO Fisheries Report 6(2), p. 562–587. [Available from CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia.]

[7] Hearn, W. S. 1982. Fish tagging: data processing, editing and storage. *In* CSIRO data base for southern bluefin tuna (*Thunnus maccoyii* (Castlenau)) (J. Majkowski, ed.), p. 8–9. CSIRO Marine Laboratories, Rep. 142. [Available from CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia.]

Analytical methods

Models Two basic models were used to analyze growth information from the tag-return data. The first was the simple VBG model:

$$l_t = L_\infty\left(1 - e^{-k(t-t_0)}\right), \qquad (1)$$

where L_∞ = the length that fish grow to asymptotically;
l_t = the length of a fish at age (or time) t;
k = the exponential rate at which the growth rate slows; and
t_0 = the hypothetical age (or time) when a fish is of length zero.

When applied to tag-return data, this equation can be used to predict the growth increment as a function of the length at release and the time at liberty:

$$\delta l = (L_\infty - l)\,(1 - e^{-k\delta t}), \qquad (2)$$

where δl = the growth increment;
δt = the time at liberty; and
l = the length of release.

Note, in this study we simplified the growth model by not accounting for seasonal growth. However, data on recaptured fish with short times at liberty were specifically deleted to ensure that our results were robust after this simplification.

Preliminary analyses of the tag-return data suggested that a simple and time invariant von Bertalanffy growth model may not provide an adequate description of the growth rate for SBT. These preliminary analyses suggested

1. Growth rates in the 1960s and the 1980s were not equal;
2. There were systematic deviations from a VBG curve, possibly corresponding to different growth processes or models for adults and juveniles.

Consequently, in the present study, we considered a more complex model than the simple VBG and conducted separate, as well as combined, analyses of the tag data from the two periods. The more complex model selected was the two-phase growth model developed by Bayliff et al. (1991). In this model, fish grow according to one model (or parameter set) up to a certain length and according to another thereafter. In our analyses, we assumed that fish have VBG throughout their lives but grow according to one set of VBG parameters ($L_{\infty 1}$ and k_1) up to length L^* and according to a second set ($L_{\infty 2}$ and k_2) at larger sizes, the two-phase VBG model. Thus, the predicted length as a function of time for this model is

$$l_t = \begin{cases} L_{\infty 1}\left(1 - e^{-k_1(t-t_0)}\right) & \text{for } t \le t^* \\ L^* + (L_{\infty 2} - L^*)\left(1 - e^{-k_2(t-t_0)}\right) & \text{for } t > t^* \end{cases}, \qquad (3)$$

where t^* = the predicted time for a fish to reach L^*.

Note that t^* can be solved for in terms of four of the parameters of the model (t_0, k_1, $L_{\infty 1}$, and L^*):

$$t^* = t_0 - \frac{1}{k_1}\log\left(1 - \frac{L^*}{L_{\infty 1}}\right), \qquad (4)$$

where $$t_0 = t_1 + \frac{1}{k_1}\log\left(1 - \frac{l_{t_1}}{L_{\infty 1}}\right),$$

and l_{t1}= the length of a fish at the time of tagging, t_1.

As with this simple VBG model, Equation 3 can be solved to predict the growth increment as a function of the release length and the time of liberty $\delta t = t_2 - t_1$:

$$\delta l = \begin{cases} (L_{\infty 1} - l_{t1})(1 - e^{-k_1\delta t}) & \text{if } t_2 \le t^* \\ (L^* - l_{t1}) + & \\ (L_{\infty 2} - L^*)\left(1 - e^{-k_2(\delta t - (t^* - t_1))}\right) & \text{for } t_1 < t^* \text{ and } t_2 > t^* \\ (L_{\infty 2} - l_{t1})(1 - e^{-k_2\delta t}) & \text{if } t_1 \ge t^*. \end{cases} \qquad (5)$$

It should be noted that in some of the analyses considered below, the estimate of $L_{\infty 1}$ did not converge (i.e. the estimate for $L_{\infty 1}$ was essentially infinite). In such cases, the estimated growth rate is linear, with growth rate R_1, and for the first phase we replaced the von Bertalanffy growth function with a simple linear one:

$$\delta l = R_1\delta t,$$

and $$t^* = t_1 - (L^* - l_{t1})/R_1. \qquad (6)$$

Model-fitting procedure A large body of literature exists on statistical approaches for estimating growth from tag-return data (e.g. Fabens, 1965; Sainsbury, 1980; Kirkwood and Somers, 1984; Francis, 1988; James, 1991; Hampton, 1991; Wang et al., 1995). The most appropriate approach depends on the error structure assumed for the model. We followed the maximum-likelihood approach and general error structure described by Hampton (1991). The measured growth increment of fish "*i*" is

$$\delta l_i = E[\delta l_i] + \varepsilon_i + e_i, \tag{7}$$

where ε_i is due to measurement error in the observed growth increment (i.e. the combined effect of any errors in measuring the lengths at the time of release and recapture) and e_i is due to process or model error. The latter may be a function of l_1, δt, δl, and the model parameters.

For the measurement error component, we allowed for different variances, depending upon whether the recaptured fish was measured by an independent and scientifically trained individual or by a fisherman. Scientifically trained individuals (i.e. scientists) included fishery observers, port samplers, and CSIRO staff. We assumed that the measurement error was normally distributed, with mean zero and variance σ_x^2, where x is one of f or s for recaptured fish measured by fishermen or scientists.

The choice of the functional form for the process error in growth models is a complex issue. One approach has been to consider that process error stems from variability among individuals in the expected value of the growth parameters (e.g. Sainsbury, 1980; Hampton, 1991; Wang et al., 1995). This approach in the case of the two-phase VBG model would result in many potential structures for the process error component because there could be individual variability in the expected value of any single or possible combination of parameters (of which there are 25 combinations). There is little theoretical basis for deciding which of these 25 combinations to use. As an alternative, we selected a more empirical approach. A function that increases with longer times at liberty seemed appropriate, and was also consistent with preliminary analyses. We explored both linear and quadratic functional relationships between the times at liberty and the process error component. The quadratic term was found to be insignificant, and therefore we chose to report only results for a simple linear functional relationship, namely $\sigma_m^2\,\delta t$. Hence the corresponding variance of the expected growth increment of fish i is $V(\delta l_i) = \sigma_x^2 + \sigma_m^2\,\delta t_i$. It should be noted that without independent data on measurement error any constant component in process error would be totally confounded with the measurement error term in the model. Therefore, σ_x^2 should be considered as a combined measurement and process error term. Both σ_x and σ_m were estimated empirically by maximum likelihood tag increment data.

Assuming a Gaussian error distribution, the likelihood function is

$$L = \prod_{i=1}^{n} \{2\pi V(\delta l_i)\}^{\frac{1}{2}} \exp\left\{ -\frac{\{\delta l_i - E[\delta l_i]\}^2}{2V(\delta l_i)} \right\}. \tag{8}$$

The estimates of the parameters are found by minimizing

$$-\ln(L) = \frac{1}{2}\sum_{i=1}^{n}\left[\log\{2\pi V(\delta l_i)\} + \frac{\{\delta l_i - E[\delta l_i]\}^2}{V(\delta l_i)} \right]. \tag{9}$$

The minimum value was obtained for all models by using the minimizing subroutine MINIMD (programmed by D.E. Shaw, CSIRO Div. Maths. and Stats.), which uses the Nelder and Mead (1965) method.

Model selection The estimation of the full two-phase VBG models across both tagging periods contains 16 parameters (five model parameters plus three variance parameters for each time period). We examined a variety of alternative hypotheses to test whether the number of parameters could be reduced by eliminating some or equating them. For the model parameters, we considered whether the L_∞ or k terms were equal either between time periods or between the first and second phases within a time period. We also considered the simple VBG model, for which L^* doesn't exist.

For the L^* parameter, we considered whether the estimates were different between the two time periods. We also examined models in which the value of L^* was determined by assuming that the expected growth rate for a fish of length L^* was equal for both growth phases (i.e. by assuming that the changes in growth rates as a function of length is a continuous function). Under this assumption

$$L^* = \frac{L_{\infty 1}k_1 - L_{\infty 2}k_2}{k_1 - k_2}. \tag{10}$$

This model is referred to as the continuous rate two-phase model in the "Results" section. However, this model is not smooth because it has a discontinuity in the derivative of the growth rate at L^*. For the variance parameters, we considered whether any of them could be eliminated and also whether $\sigma_s = \sigma_f$. We used the log-ratio test and AIC criterion (Akaike, 1974) to identify the most parsimonious model.

Results

Best fits to the 1960s and 1980s data

Table 1 contains the maximum likelihood solutions for various assumptions when fitting growth models to either the 1960s or 1980s tag-return data separately. Using the AIC criteria, we found the best-fit model for the 1960s tag-return data was one with linear growth in the first phase and with the change between the two phases at approximately 74 cm (row 1, Table 1A). The fit to this model compared with all other parameter combinations yielded both the lowest AIC and negative log-likelihood values. The fit, however, was only marginally better then the fit (row 3, Table 1A) to the two-phase VBG curve with common k parameters (e.g. where the difference in the negative log-likelihood values is 1.21). Except for the first phase growth parameters, the estimates for the other parameters are nearly identical between these two models. This similarity reflects the fact that growth is nearly linear over the initial part of a VBG curve. Thus, by having a relatively high $L_{\infty 1}$ (271 cm), essentially similar growth rates can be achieved up through the 74 cm size range when $k_1 = k_2$, as compared with linear growth in the first phase. It should

Table 1

(**A**) Estimation of SBT growth parameters, and tests, from 1960s tag-return data with time at liberty of at least 270 days; (**B**) Estimation of SBT growth parameters, and tests, from 1980s tag-return data with time at liberty of at least 270 days. "na" = not applicable because this is the normal von Bertalanffy curve, i.e. with only one phase.

Common parameters	Number of parameters	$L_{\infty1}$	k_1	$L_{\infty2}$	k_2	L^*	σ_s	σ_f	σ_m	–Log likelihood	AIC
A											
none	6	22.23[1]	0.0000	210.90	0.1063	74.24	0.000	3.122	2.992	2055.53	4123.07[2]
$L_{\infty1}=L_{\infty2}$	6	212.73	0.1451	212.73	0.1044	75.75	0.000	3.134	2.999	2057.39	4126.77
$k_1=k_2$	6	271.35	0.1060	211.35	0.1060	74.71	0.000	3.130	2.997	2056.74	4125.49
$L_{\infty1}=L_{\infty2}$ $k_1=k_2$	5	172.67	0.1723	172.67	0.1723	na	2.201	3.782	2.855	2099.04	4208.08
continuous rate	6	114.14	0.4289	205.45	0.1128	81.55	0.000	3.203	3.021	2065.89	4143.78
$\sigma_m=0$	7	760.47	0.03425	191.33	0.1330	70.00	3.478	5.258	0.000	2088.19	4190.39
$\sigma_s=\sigma_f$	6	22.20	0.0000	209.65	0.1085	74.04	2.301	2.301	3.180	2068.33	4148.66
$\sigma_s=\sigma_f=0$	6	454.10	0.05660	214.26	0.1033	74.70	0.000	0.000	3.752	2071.57	4155.15
B											
none	8	226.70	0.1649	182.52	0.1841	84.90	2.305	4.501	3.018	4509.99	9035.97
$L_{\infty1}=L_{\infty2}$	7	183.09	0.2276	183.09	0.1832	85.65	2.266	4.497	3.031	4510.44	9034.88
$k_1=k_2$	7	210.24	0.1841	182.61	0.1841	84.99	2.276	4.492	3.030	4510.02	9034.03[3]
$L_{\infty1}=L_{\infty2}$ $k_1=k_2$	5	156.45	0.2884	156.45	0.2884	na	1.626	4.209	3.405	4530.88	9071.76
continuous rate	7	141.07	0.3590	182.25	0.1842	97.70	2.148	4.473	3.085	4514.54	9043.09
$\sigma_m=0$	6	206.71	0.1883	180.82	0.1883	84.85	4.149	5.920	0.000	4526.06	9064.11
$\sigma_s=\sigma_f$	6	210.74	0.1858	182.23	0.1858	85.36	3.948	3.948	3.183	4529.25	9070.49
$\sigma_s=\sigma_f=0$	5	209.46	0.1875	181.49	0.1875	85.30	0.000	0.000	4.737	4545.25	9100.49

[1] Here k_1 is zero,i.e. the growth rate is constant in the first phase; therefore we give the estimate of the growth rate instead of $L_{\infty1}$.

[2] The least AIC value for estimates from the 1960s data. Na= not applicable because this is the normal von Bertalanffy curve, i.e. with only one phase.

[3] The least AIC value for estimates from the 1980s data.

also be noted that the two-phase VBG model with common L_∞ (row 2, Table 1A). was very similar to the common k parameterization, reflecting the high correlation between L_∞ and k in the VBG models. For the 1960s, the continuous two-phase VBG model was rejected, $P<0.005$ (row 5, Table 1A).

For the 1980s data, the best-fit model based on the AIC values was for the two-phase VBG model with a common value for the k parameter in both phases (row 3, Table 1B). The estimate of the size at which the change between the two phases occurs was 85 cm (compared to the estimate of 74 cm for the 1960s data). As with the results of the 1960s data, the common-k model, common- L_∞ model, and the full two-phase model yielded very similar values for both the likelihood and parameter estimates in the second phase, but not for those in the first phase. This similarity reflects the high correlation between k and L_∞ in the VBG model, so that over the limited size range below L^* nearly identical growth rates can be achieved in the common-k model by decreasing the value of $L_{\infty1}$. For the 1980s (as with the 1960s), the continuous two-phase VBG model (7 parameters), was rejected, $P<0.005$ (row 5, Table 1B).

For both the 1960s and 1980s data, the two-phase model provided a substantially and significantly better fit to the tag return data than a simple VBG model. This can be seen in Table 1 (A and B) by comparing the negative log-likelihood and AIC values for the simple VBG model (row 4) with any that include a two-phase component, particularly the continuous rate two-phase VBG model. We also fitted a smooth Richards' (1959) growth model (a generalization of the VBG model) to the data, which fitted better than the simple VBG model, but worse than the two-phase VBG models.

Note, however, that the log-ratio test and AIC criterion may not be fully applicable for testing the differences between the simple and two-phase VBG models because the simple VBG model can arise in more than one way as a submodel of the two-phase model (e.g. with common L_∞ and k parameters or from L^* equaling zero or infinity) (Davies, 1977, 1987). Nevertheless, the large magnitude of the differences in the log-likelihood values indicates a significance difference.

For the 1960s data, it should be noted that the scientist measurement error (σ_s) was estimated to be essentially zero when it was included as an explicit term in several of the models. In these cases, we refitted the models excluding this parameter. Common sense dictates that measurement errors would not be zero. The most informative data

Table 2

Comparison of SBT growth parameter estimates for the 1960s and 1980s, between absolute maximum likelihood and local maxima likelihood.

Common parameters	Number of parameters	$L_{\infty 1}$	k_1	$L_{\infty 2}$	k_2	L^*	σ_s	σ_f	σ_m	–Log likelihood	AIC
1960s											
none	6	22.23[1]	0.0000	210.90	0.1063	74.24	0.000	3.122	2.992	2055.53	4123.07
none	8	118.08	0.3957	186.04	0.1500	91.23	1.061	3.398	2.855	2062.76	4141.51
1980s											
k_1=k_2	7	210.24	0.1841	182.61	0.1841	84.99	2.276	4.492	3.030	4510.02	9034.03
k_1=k_2	7	145.37	0.3371	169.03	0.3371	120.47	2.293	4.514	3.025	4512.98	9039.96

[1] Here k_1 is zero, i.e. the growth rate is constant in the first phase; therefore we give the estmate of the growth rate instead of $L_{\infty 1}$.

on measurement error would come from fish with short times at liberty because in these cases the amount of process error would be small. However, as explained above, fish with times at liberty of less than 270 days were excluded to eliminate seasonal effects. Process and measurement errors are partially confounded in the model. The estimation procedure could not distinguish an additional constant component to the linear, temporally increasing process error from the measurement error for recaptured fish measured by scientists. For the 1980s data, the estimation procedure was able to estimate a nonzero value for the scientist measurement error. The results for the 1980 returns suggest that the measurement error for the scientists was about 50% of that for fishermen.

For both the 1960s and 1980s data, the estimation procedure is able to distinguish between fishermen and scientist measurement error. The assumption that the measurement error of fishermen and scientists are the same is rejected by a statistical test (i.e. the second last line of both Table 1, A and B).

Examination of the residuals indicated no systematic lack of fit in either the 1960s or 1980s data (Fig. 1, A–D).

Shape of the likelihood function

It is worth noting that the likelihood function is bimodal with respect to the parameter determining the length at which growth changes between the two phases (L^*). Figure 2 shows the negative log-likelihood (*–LL*) values as a function of L^* for the 1960s and 1980s data for the best-fit model. For the 1960s data, the *–LL* function has an absolute minimum at $L^* = 74$ cm and a second, local minimum at $L^* = 91$ cm. For the 1980 data, the absolute minimum occurs at $L^* = 85$ cm and the second, local minimum at $L^* = 120$ cm.

Monte Carlo and bootstrap simulations were conducted to evaluate the bimodal nature of the likelihood function. The Monte Carlo simulations were done by assuming the two-phase VBG growth model and were conditional on the SBT release lengths. Both types of simulations confirmed that the minima with the lowest absolute value for the negative log-likelihood function would switch between individual realizations within the simulations. Only the results of the bootstrap simulations are presented in this article. These were based on 1000 individual simulations for which the tag increment data were randomly sampled with replacement. For each individual simulation, the value of L^* that yielded the absolute minimum value for the negative log-likelihood function was determined. For the 1960s data, the best-fit estimate of L^* was near 74 cm in 930 of the simulations and 91 cm in 70. For the 1980 data, the absolute minimum in the negative log-likelihood function occurred 767 times when L^* was near 85 cm and 233 times when L^* was near 120 cm (Fig. 3). Thus, although the lower value for L^* was the most likely for both the 1960s and 1980s data, the 95% confidence intervals based on the bootstrap results would encompass both values. The estimated value of the other parameters determining the expected growth curve are correlated with that of L^*. Thus, the alternative minima in the log-likelihood function are associated with substantially different estimates for the k and L_∞ parameters (Table 2). This in turn has implications for possible biological interpretations of the parameter estimates (see below).

Joint analyses of the 1960s and 1980s data

Results of jointly modeling the 1960s and 1980s tag return data to test for common parameters are presented in Table 3. The model error (σ_m) was the only parameter found not to be significantly different in the combined analyses. Having a single parameter value for the model error component had virtually no effect on the parameters determining the expected growth rates, compared to those estimated in the separate analyses.

Comparison of 1960s and 1980s growth rates

The fact that all of the parameters that describe the expected growth rates significantly differ for the 1960s and 1980s data indicates that SBT growth rate changed between these two periods. For the best-fit solutions, the

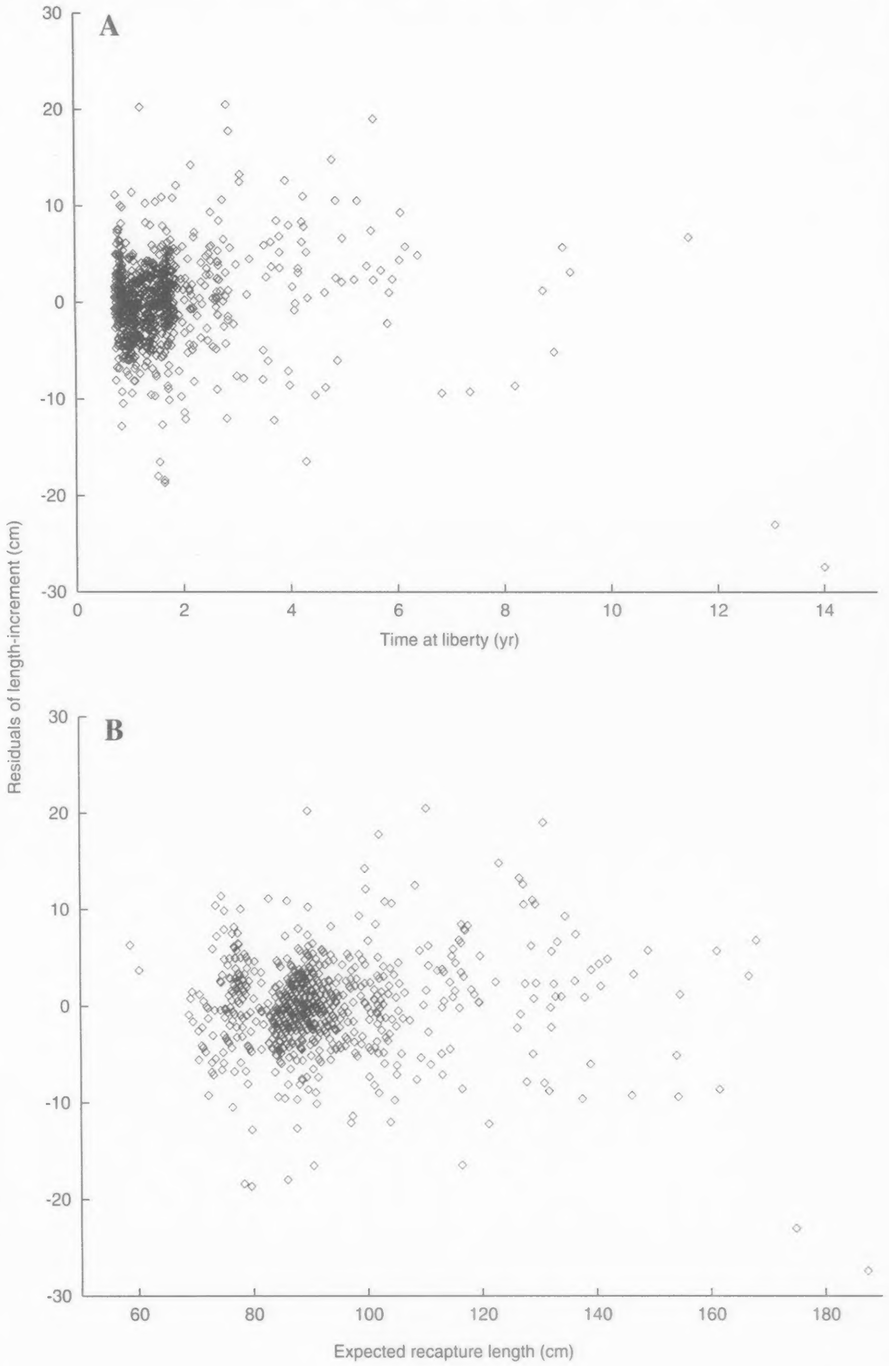

Figure 1

Residual plots from the best-fit models in Table 1 to the 1960s and 1980s tagging data: (**A**) residuals for time at liberty for the 1960s; (**B**) residuals for expected recapture lengths for the 1960s; (**C**) residuals for time at liberty for the 1980s; (**D**) residuals for expected recapture lengths for the 1980s.

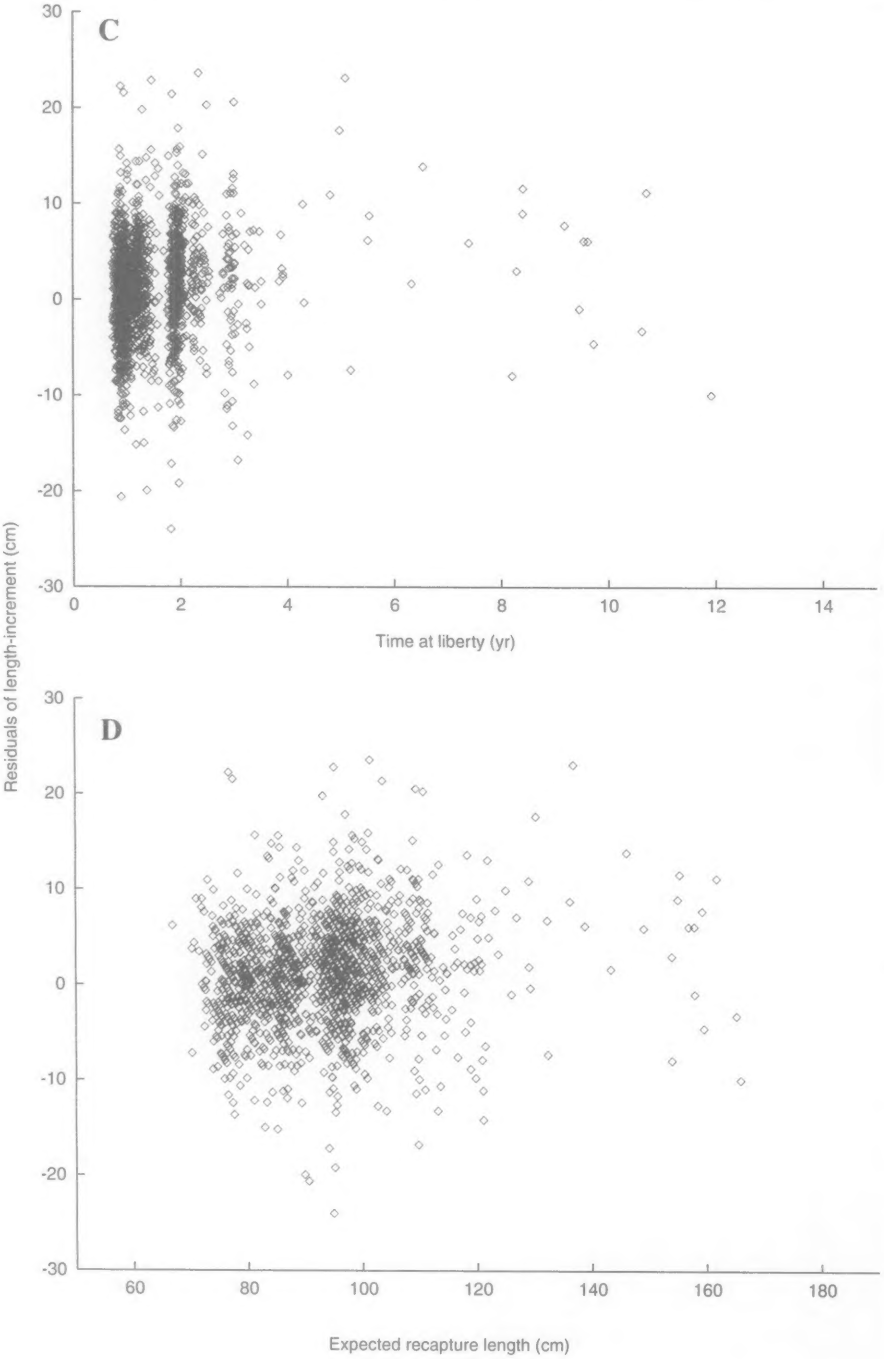

Figure 1 (continued)

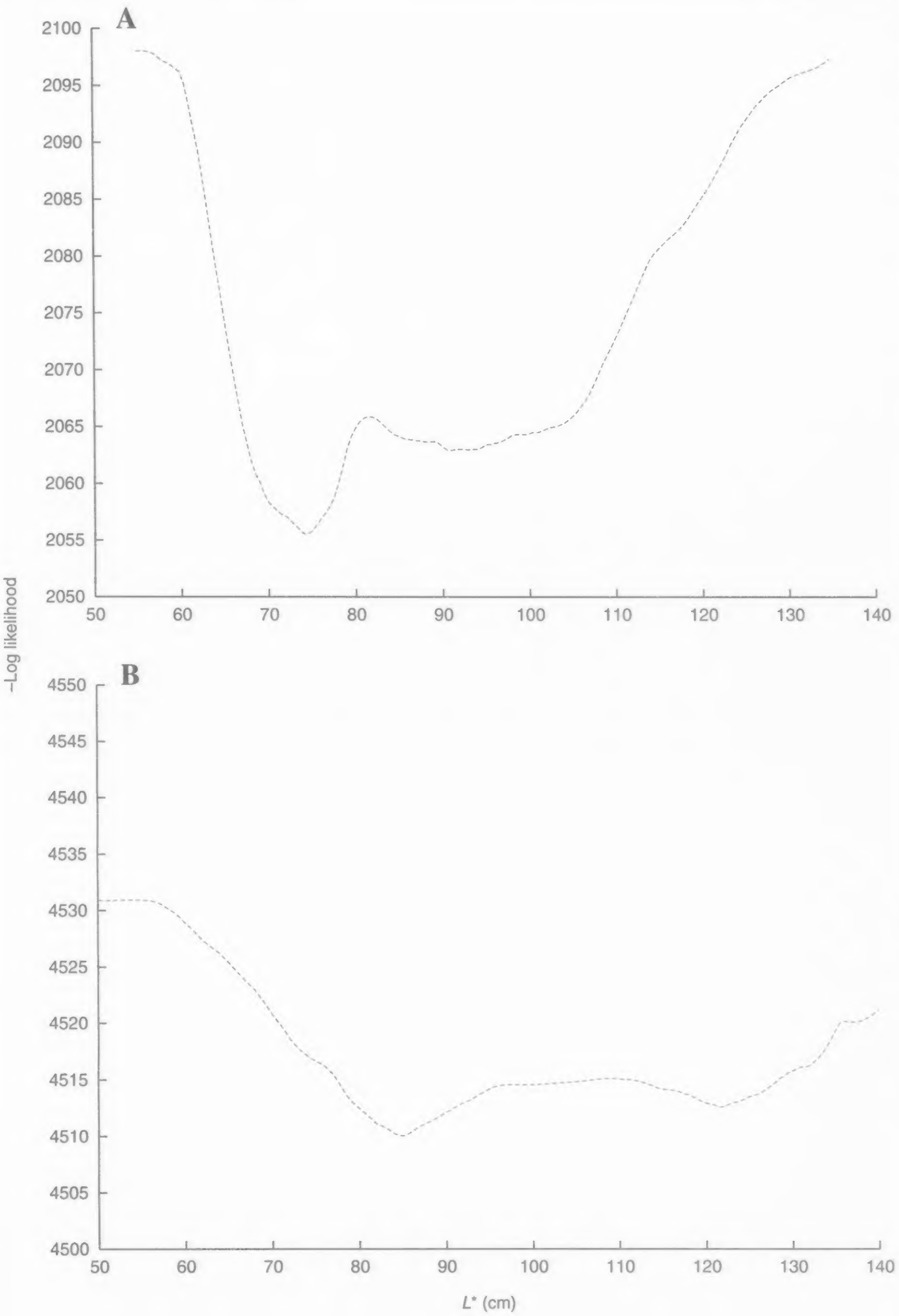

Figure 2

Negative log-likelihood value as a function of L^*: (**A**) for the 1960s; (**B**) for the 1980s.

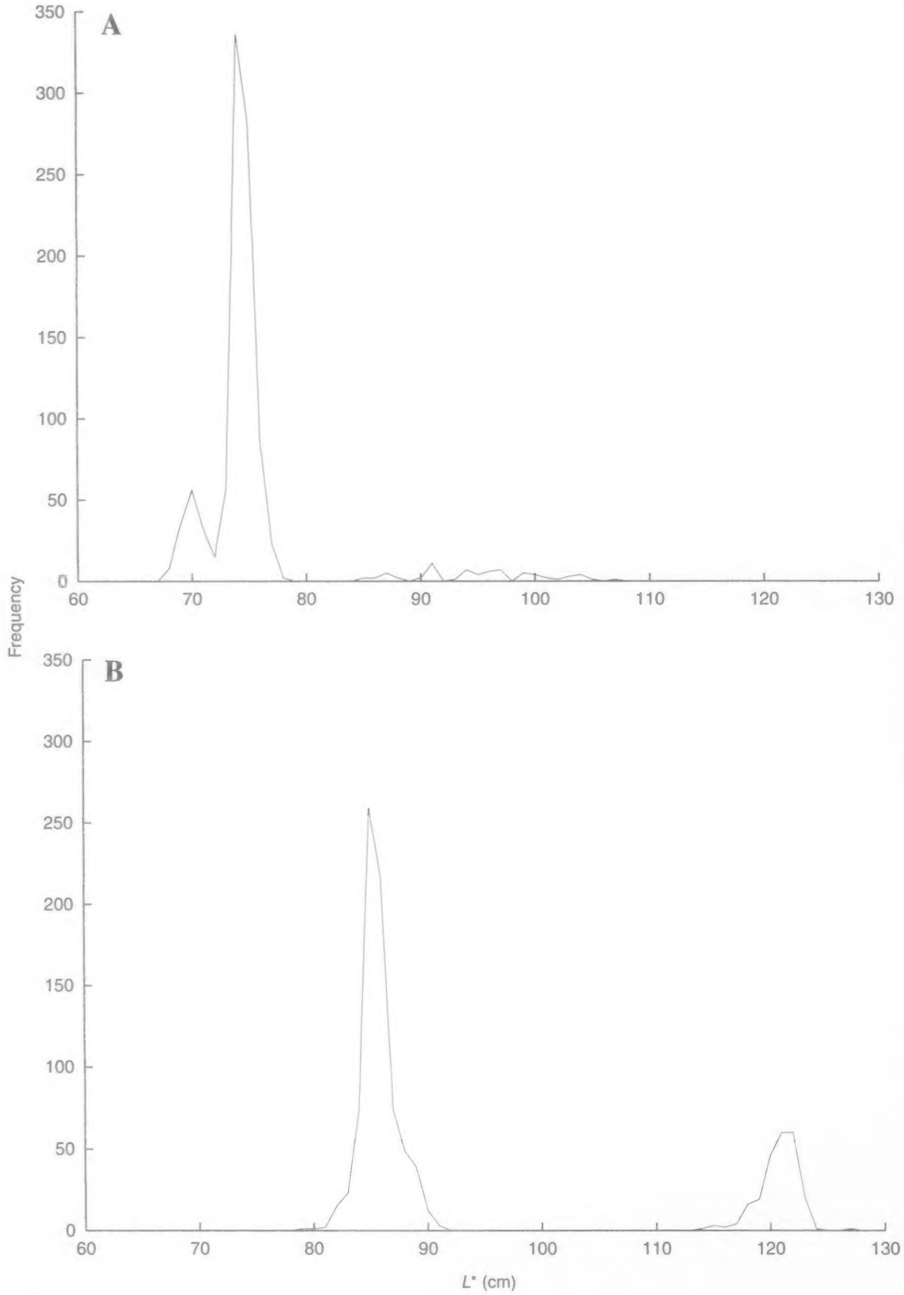

Figure 3

Frequency distribution for the estimates of L^* from 1000 bootstrap simulation results: (**A**) for the 1960s; (**B**) for the 1980s.

Table 3

Southern bluefin tuna growth parameters and tests, from jointly analyzing the 1960s and 1980s data.

Common parameters	Number of parameters	$L_{\infty 1}$	k_1	$L_{\infty 2}$	k_2	L^*	σ_s	σ_f	σ_m	–Log likelihood	AIC
none (60)	13	22.23[1]	0.0000	210.90	0.1063	74.24	0.000	3.122	2.992		
(80)		210.24	0.1841	182.61	0.1841	84.99	2.273	4.496	3.030	6565.55	13157.10
$\sigma_m 60=\sigma_m 80$	12	22.23	0.0000	210.98	0.1062	74.25	0.000	3.115	2.998		
		210.31	0.1840	182.67	0.1840	85.00	2.309	4.514	2.998	6565.56	13155.11
$L60_{\infty 1}=L80_{\infty 1}$	12	213.29	0.1462	210.49	0.1069	75.03	0.000	3.133	3.001		
		213.29	0.1804	184.20	0.1804	85.00	2.323	4.518	3.001	6567.43	13158.85
$L60_{\infty 1}=L60_{\infty 2}=L80_{\infty 1}$	11	211.41	0.1480	211.41	0.1060	75.08	0.000	3.128	3.004		
		211.41	0.1827	183.24	0.1827	85.00	2.315	4.515	3.004	6567.44	13156.87
$k60_1=k80_1$	12	185.24	0.1804	210.46	0.1069	75.11	0.000	3.119	3.008		
		213.26	0.1804	184.21	0.1804	85.01	2.325	4.510	3.008	6568.07	13160.15
$L60_{\infty 2}=L80_{\infty 2}$	11	22.20	0.0000	195.25	0.1232	73.74	0.000	3.120	3.010		
		233.55	0.1584	195.25	0.1584	85.22	2.302	4.516	3.010	6568.89	13159.78
$k60_2=k80_2$	11	23.85	0.0000	186.76	0.1374	70.48	0.000	3.097	3.044		
		258.76	0.1374	207.04	0.1374	86.23	2.262	4.495	3.044	6575.52	13173.03
$L^*60=L^*80$	12	110.51	0.4707	196.71	0.1269	85.45	0.000	3.196	3.014		
		211.13	0.1827	182.97	0.1827	85.45	2.306	4.505	3.014	6574.09	13172.19
$\sigma_s 60=\sigma_s 80$	12	22.22	0.0000	210.59	0.1072	74.10	1.602	3.023	3.068		
		209.66	0.1842	182.49	0.1842	84.94	1.602	4.472	3.068	6570.46	13164.92
$\sigma_f 60=\sigma_f 80$	11	22.28	0.0000	210.43	0.1064	74.23	0.000	4.174	2.975		
		210.40	0.1844	182.62	0.1844	85.02	2.394	4.174	2.975	6577.96	13177.91

[1] Here k_1 is zero, i.e. the growth rate is constant in the first phase; therefore we give the estimate of the growth rate instead of $L_{\infty 1}$.

SBT growth rates in the 1960s are estimated to be less than those in the 1980s up to 144 cm (Fig. 4). Comparison of the 1960s and 1980s expected growth curves over time for a 55-cm fish are presented in Figure 5. In making this comparison, we assumed that a 55-cm fish is approximately one year of age (Anonymous[5]) and that size at age one did not change between the 1960s and 1980s, as supported by length-frequency data from these two time periods (Leigh and Hearn, 2000; Anonymous[5]). Thus, Figure 5 can also be considered as an estimate of the expected length-at-age curve. Figure 5 indicates that the overall expected growth was significantly faster in the 1980s than in the 1960s, so that a fish of 55 cm or age 1 would take approximately four years in the 1960s to achieve the same length that would have been achieved in three years in the 1980s.

A feature of the best-fitted estimated growth parameters is that the expected growth curves intersect at ~170 cm, so that after age 13 a fish from the 1960s is estimated to be larger than a fish from the 1980s. This crossover is driven primarily by the difference in the estimates of $L_{\infty 2}$. The standard log-likelihood test indicates a low probability, $P=0.01$, that $L_{\infty 2}$ for the 1960s and 1980s are the same. However, the analyses of the bootstrap estimates of $L_{\infty 2}$ indicate that the estimates are bimodal, reflecting the bimodal distribution of L^*. Random sampling from the bootstrap distributions for $L_{\infty 2}$ showed that in 6.1% of cases the 1960s $L_{\infty 2}$ estimate was less than the 1980s estimate. For a two-sided test at the 5% significant level, at least 2.5% (and at most 97.5%) of the bootstrap samples would have been expected to have the 1960s $L_{\infty 2}$ less than that of the 1980s to justify the hypothesis that the two $L_{\infty 2}$ are equal. Thus, based on the bootstrap results, the hypothesis of equality cannot be rejected. Most of the 6.1% of cases are associated with the 1960s $L_{\infty 2}$ less than 180 cm, which are in turn associated with the upper mode of L^* in Figure 3A, i.e. near $L^* = 91$ cm. It is worth noting that only three recapture lengths were greater than 170 cm. There are, therefore, very minimal data for estimating growth rates beyond 170 cm and for precisely estimating $L_{\infty 2}$.

Discussion

The results in this study indicate that the traditional VBG model does not provide an adequate representation of growth in SBT. There appears to be a significant change in the pattern of growth in relation to a VBG curve during the juvenile stages of the SBT life cycle. This, in turn, may be related to the transition from a tightly schooling fish that spends substantial time in near and surface shore waters

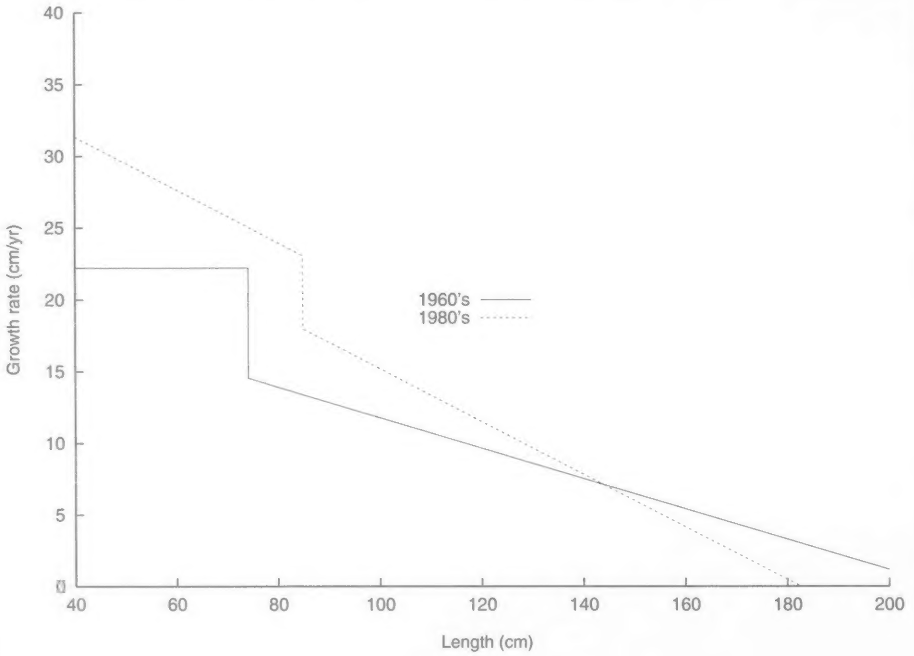

Figure 4

Comparison of the 1960s and 1980s best-fit estimates of southern bluefin tuna growth rates as a function of length.

to one that is found primarily in more offshore and deeper waters. In this regard, recent information from archival tags indicates that SBT between 80 and 90 cm (about two to three years old) commonly migrate during winter months to offshore oceanic waters in the Indian Ocean and the Tasman Sea and begin to feed at substantial depth (Gunn and Block, 2001). In contrast, catches and samples off Albany, Western Australia, show that many SBT less than 70 cm stay in nearshore Australian waters during winter (Hynd, 1965; Murphy[8]; and release data analyzed in this study). Thus, the growth changes estimated to be near $L^* = 80$ cm may correspond to a marked change in the SBT behavior during these winter months.

The von Bertalanffy growth equation and its modifications have been the standard for modeling tuna growth. The life history dynamics for most tuna species (e.g. north Pacific bluefin, albacore, bigeye, and yellowfin tuna) have a bimodal component analogous to that of SBT. Thus, juveniles are frequently found in densely packed surface schools, whereas at larger sizes individuals are rarely found near the surface and appear not to occur in densely packed schools (although there is little direct information on schooling for these larger fish). Moreover, mature tuna expend considerable energy in the spawning process, and in some cases swim thousands of kilometers and incur considerable weight losses during spawning (Warashina and Hisada, 1970). Bayliff et al. (1991) also found that growth models with a rate discontinuity at a certain size provided a better fit to Pacific northern bluefin tuna tag-return data than a simple continuous growth model. The extent to which this may be a general phenomenon in tuna or other fish species with marked changes in habitat use with age is not clear. However, the results from our study and those of Bayliff et al. (1991) suggest that a growth rate with a discontinuity at a certain size may be more common than existing modeling of growth may indicate. Complex growth models, which deviated from a simple continuous growth curve, have generally not been considered, and the available data, in many cases, may not have sufficient power to be able to statistically identify more complex growth processes if they exist.

Although the complex two-stage growth model used in our study clearly provided a substantial and significant improvement in fit to the growth-increment data, the model itself presents problems in terms of the biological interpretation of the parameter estimates for L^*. The bimodal nature of the likelihood function means that the size and

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[8] Murphy, G. I. 1979. Southern bluefin tuna. Aust. CSIRO Div. Fish. Oceanogr. Fishery Situation Report 1, 10 p. [Available from CSIRO Marine Research, GPO Box 1538 Hobart 7000, Australia.]

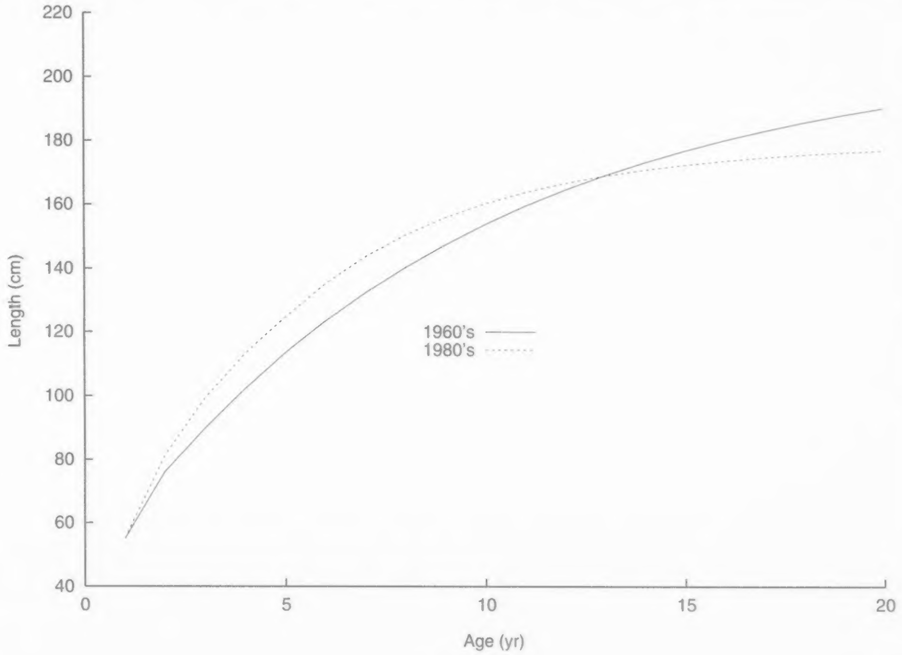

Figure 5

Comparison of the 1960s and 1980s best-fit estimates for the expected length of southern bluefin tuna as a function of age, assuming that the expected length of an age-1 fish is 55 cm.

age where the change in growth occurs is not well defined. This, in turn, confounds the evaluation of the plausibility of different specific possible biological hypotheses underlying the change. Moreover, although the change in growth patterns may be quite rapid, a large discontinuity in the growth rates at a specific length seems unrealistic. The continuous two-stage VBG model did not fit the 1960s and 1980s data as well as the discontinuous two-stage VBG models. However, the two-phase VBG models fitted the data better than the simple von Bertalanffy growth curve (Table 1, A and B) and its generalization—the simple Richards' (1959) curve (senior author, unpubl. results).

From both the statistical estimation and biological perspective, we think there is scope for the development of more appropriate complex growth models. In this context, there is also need for the development of estimation procedures for these complex models that can take into account alternative error structures that allow for individual variability in the growth rate parameters (e.g. Sainsbury, 1980; James, 1991; Wang et al., 1995).

In the joint analysis of the 1960s and 1980s data, σ_m was the only parameter found not to be significantly different between the two data sets. However, caution is warranted in any comparison and interpretation of growth curves determining parameter values because of the well-known negative correlation between k and L_∞ of the VBG growth model and the bimodal nature of the likelihood surface, as already noted. In particular, the differences in the estimates of $L_{\infty 2}$ should not be taken as strong evidence that the asymptotic growth of SBT decreased or that there was a crossover in the growth rates. These complex growth changes are difficult to explain from a biological perspective and, as noted above, the bootstrap results indicate that the hypothesis that the $L_{\infty 2}$ parameters are equal cannot be rejected. Moreover, we would note that there is a paucity of tag return data for larger fish. A total of only seven tags were recovered from fish with lengths exceeding 165 cm and only three for fish with lengths in excess of 170 cm. Fitting VBG models does not provide reliable estimates of growth when extrapolated beyond the range of the data because of the large negative correlation between k and L_∞. We, therefore, do not think that the current data are sufficient to determine whether, in fact, $L_{\infty 2}$ differed between the 1960s and 1980s.

One of the primary applications of the estimated SBT growth curves is to provide estimates of the age distribution of commercial catch in stock assessments based on catch-at-age analyses (e.g. Anonymous[8]). The predicted growth curves (assuming that an age-1 fish is 55 cm) indicate that the estimated ages of 165-cm fish have diverged by about a year for the curve based on a common $L_{\infty 2}$ compared with those for which $L_{\infty 2}$ is allowed to differ between the 1960s and 1980s. For smaller sizes, the divergence is substantially less (e.g. for fish 140 cm or less the divergence is less than three months). In terms of using the growth rate data to estimate ages from lengths, these results indicate that for the older reproducing fish the results will be highly sensitive to assumptions about $L_{\infty 2}$.

The results from these tagging studies clearly show that growth rates for SBT hatched in the 1980s had increased in relation to those cohorts hatched in the 1960s. The increase in growth rates is substantial, so that a fish, on average, would have been expected to take four years to grow from 55 cm to 111 cm in the 1960s, but only three years to do so in the 1980s. In other words, after age 4 there is a difference of about one year in the expected age of a fish of similar length, and this difference persisted over the size range for which meaningful recapture data were available. The change in growth and its magnitude are consistent with the analyses in Leigh and Hearn (2000) of the modes in length-frequency distributions of juvenile fish captured in the Australian surface fishery. The underlying causes of the change in SBT growth rates are unknown. They could be associated with changes in environmental conditions, population size, or a combination of the two. The change in SBT growth rates between the 1960s and 1980s is associated with very substantial declines in both the adult and juvenile components of the SBT stock (Polacheck et al.[1]; Anonymous[9]).

There is an increasing number of examples in which growth rates have been reported to be inversely correlated to fish population numbers because of intraspecific competition. For example, Le Cren (1958) documented an increase in the growth rate of perch after a planned reduction of a lake population. In a converse case, Kaeriyama (1996) reported a decline in the growth rate of Japanese chum salmon following a many-fold increase in its population size because of a most successful hatchery enhancement scheme. Other accounts are published in Southward (1967), de Veen (1976), Toresen (1990), Ross and Nelson (1992), and Sinclair and Swain (1996). However, the reports are mainly on species for which direct aging data are reliable and regularly collected over a lengthy period, or the fish are hatchery reared.

The hypothesis that the increase in SBT growth rates was the result of the marked reduction in SBT population size would seem plausible, given the similar associations that have been found in a number of fisheries phenomena. As discussed in Leigh and Hearn (2000), changes in juvenile SBT growth rates based on analyses of length-frequency data are also consistent with the change having a density-dependent component. In this regard, it is worth noting that preliminary analyses of tag return data from the 1990s indicate that growth rates in the 1990s were similar to those in the 1980s (Polacheck and Preece[10]). Thus, these preliminary results are also consistent with the change in growth being a density-dependent response as both juvenile and adult SBT abundances remained at low levels during this period (e.g. Anonymous[9]; Polacheck and Preece[10]). Large uncertainty exists about possible recovery of the SBT stock in the near future (e.g. Anonymous[9]), but continued monitoring of SBT growth may provide one indicator of stock recovery.

To simplify our investigation we did not consider seasonal growth. We avoided possible bias, due to seasonal growth, by analyzing data only from fish with times at liberty more than or equal to 270 days. This restriction provided an efficient mechanism to focus on the long-term growth process and was effective because the resultant sets were large. Large numbers of recaptured fish with reliable information and times at liberty more than 9 months seem rare for other tunas, in which case the added complication of accounting for possible seasonable growth would be required to ensure the robustness of the results.

The analyses in this paper represent the first documented examples of substantial temporal changes in growth rates that persisted for an extended portion of the life span in a large pelagic tuna resource. For tuna stocks in general, estimates of growth rates play a major role in stock assessments and in the subsequent management advice derived from these assessments.

Acknowledgments

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Life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Richardson, 1836) off the southeastern United States

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Abstract—The life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) was described from 1093 specimens collected from Virginia to northern Florida between April 1997 and March 1999. Longitudinally sectioned vertebral centra were used to age each specimen, and the periodicity of circuli deposition was verified through marginal increment analysis and focus-to-increment frequency distributions. *Rhizoprionodon terraenovae* reached a maximum size of 828 mm precaudal length (PCL) and a maximum age of 11+ years. Mean back-calculated lengths-at-age ranged from 445 mm PCL at age one to 785 mm PCL at age ten for females, and 448 mm PCL at age one to 747 mm PCL at age nine for males. Observed length-at-age data (estimated to 0.1 year) yielded the following von Bertalanffy parameters estimates: L_∞= 749 mm PCL (SE=4.60), K = 0.49 (SE=0.020), and t_0=–0.94 (SE=0.046) for females; and L_∞=745 mm PCL (SE=5.93), K=0.50 (SE=0.024), and t_0=–0.91 (SE=0.052) for males. Sexual maturity was reached at age three and 611 mm PCL for females, and age three and 615 mm PCL for males. *Rhizoprionodon terraenovae* reproduced annually and had a gestation period of approximately 11 months. Litter size ranged from one to eight (mean=3.85) embyros, and increased with female PCL.

The Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) is a small carcharhinid that inhabits the coastal waters of the western North Atlantic from the Bay of Fundy to the Yucatan (Castro, 1983). It is the most common small coastal species off the southeastern U.S. coast and the Gulf of Mexico (Branstetter, 1990). This species is frequently encountered by a variety of commercial fishing gear, including bottom longline, gill net, bandit reel (used by the snapper–grouper fishery), and shrimp trawl. *Rhizoprionodon terraenovae* is also a common catch in the recreational hook-and-line fishery.

The age and growth of this species has been described in the Gulf of Mexico by Parsons (1981, 1983a, 1985) and Branstetter (1981, 1986, 1987a). Although those studies provided significant information on the age and growth of *R. terraenovae*, data were collected from 1979 to 1984, a time in which fishing pressure on the *R. terraenovae* population was probably not as high as at present (Cortes, 1995). The previous studies dealt with fishes only from the northern Gulf of Mexico, and therefore may not represent the entire stock, although the stock structure for *R. terraenovae* in the northwestern Atlantic remains unclear (Heist et al., 1996). No published age and growth studies exist for specimens collected from the southeastern U.S. Atlantic coast. The reproductive biology of this species has been studied in both the Gulf of Mexico and off the southeastern U.S. coast (Parsons, 1983b; Castro, 1988, 1993; Castro and Wourms, 1993), but the lack of concurrent age and growth data off the southeastern United States limits the utility of these data for fishery management.

Considering the importance of accurate and timely age, growth, and reproductive information to fishery management, this study had two objectives: to describe age, growth, and reproduction in the southeastern U.S. population of *R. terraenovae*; and to compare these data to those of previous studies on the same species in the Gulf of Mexico.

Materials and methods

Rhizoprionodon terraenovae (n=1093) were collected throughout the year in coastal waters from April 1997 through March 1999. Collection sites ranged from Chesapeake Bay, Virginia, to Port Canaveral, Florida (Fig. 1). The majority of specimens were collected off the coast of South Carolina. A variety of sampling gears were employed for sample collection: bottom longline (47% of specimens), otter trawl (22%), port-sampling of commercial fishing

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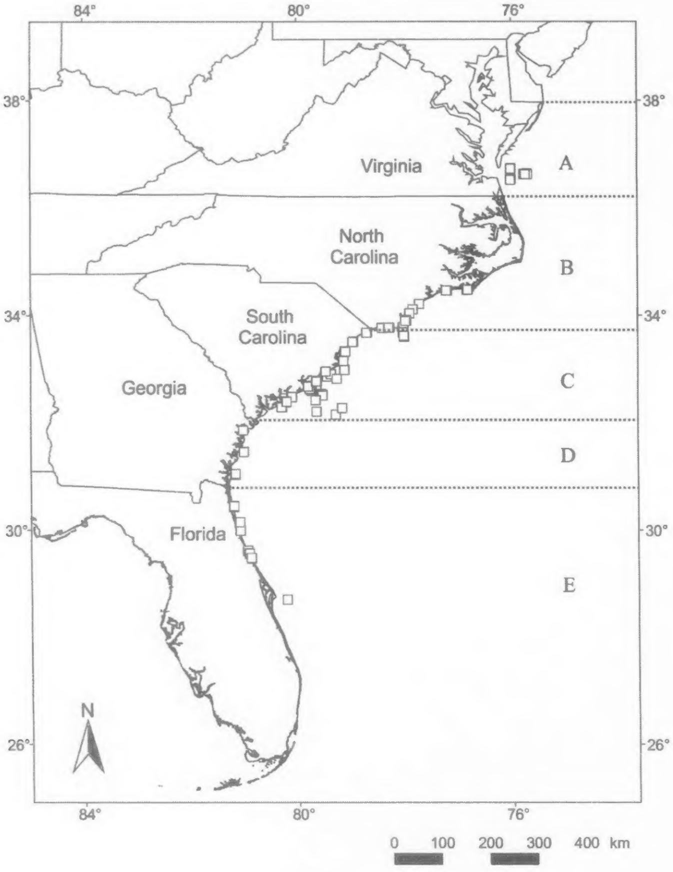

Figure 1

Sample collection sites and distribution by area (roughly equivalent to state borders) for *R. terraenovae* collected during this study, 1997–99. (□) represents locations where one or more *R. terraenovae* were captured. (**A**) = 13 males (694–793 mm PCL); (**B**) = 52 females (215–786 mm PCL), 51 males (200–765mm PCL); (**C**) = 497 females (197–813 mm PCL), 441 males (225–828 mm PCL); (**D**) = 8 females (302–763 mm PCL), 7 males (320–658 mm PCL); (**E**) = 6 females (335–738 mm PCL), 16 males (271–720 mm PCL).

vessels (16%), rod and reel (12%), gill net (3%), and other miscellaneous gear types (2%).

Following capture, the sex of each specimen was determined and the specimen was weighed (to the nearest 0.1 kg), evaluated for sexual maturity, and its body length was measured. Four body length measurements (to the nearest mm) were taken from each individual: precaudal length (PCL, measured from the tip of the snout to the anterior termination of the precaudal pit), fork length (FL), natural total length (NTL, measured with tail in a "natural" swimming position [Parsons, 1985]), and total length (TL, measured with dorsal portion of tail bent parallel to the body axis). Unless otherwise noted, precaudal lengths are used throughout this study. Regression relationships of TL, NTL, and FL on PCL were derived to facilitate comparison with other studies.

The claspers of males were measured from the clasper tip to the anterior termination of the vent. The siphon sac was measured from the base of the clasper fin (where the sac originates) to the anterior termination of the sac. The condition of the seminal vesicles was also recorded. Male maturity was indicated by calcification of the claspers and the presence of a fully formed siphon sac (Clark and von Schmidt, 1965; Parsons, 1983b). Gonadosomatic indices (GSIs, Parsons, 1983b) were calculated for male sharks with the formula

$$GSI = gonad\ weight\ (\mathrm{g})/body\ weight\ (\mathrm{g}) \times 100.$$

The ovaries and uteri of females were examined macroscopically for indicators of maturity, such as yolking eggs, embryos, or placental scars. Vitellogenic oocytes were easily identified by their bright yellow coloration in contrast to the pale white coloration of nonvitellogenic oocytes. If vitellogenic oocytes were present, the diameter of all vitellogenic oocytes in the ovary was measured (to the nearest 0.1 mm) with dial calipers. If maturing oocytes were not present, the most differentiated nonvitellogenic oocytes (which were noticeably larger that the rest of the oocytes in the ovary) were measured. Any embryos were removed from the uteri, counted, their sex determined, and measured (TL). Female maturity was determined by the presence of embryos, umbilical scars in the uterus from previous pregnancy, or the presence of large vitellogenic oocytes (greater than 15 mm diameter) nearing ovulation (Parsons, 1983b).

A segment of the vertebral column extending from the cervical region (dorsal to the branchial chamber) to the origin of the first dorsal fin was removed from each specimen and frozen. Vertebrae from the cervical portion of the spinal column were used for aging because of the shallow concavity of the intermedalia and the size similarity between adjacent centra in this region. The shallow concavity of the vertebrae facilitated processing and measurement during aging (Branstetter and McEachran, 1986). Age determination was attempted on 890 of the 1093 specimens collected during the study. Vertebrae selected for aging were separated from the frozen segment, defrosted, and soaked in 5% sodium hypochlorite for 5–30 min (depending on size) and were removed from the solution as soon as all excess connective tissue had been dissolved. A longitudinal section approximately 500 µm thick was cut from the center of each vertebrae with a Mark-V wafering saw and allowed to air-dry for at least 24 h. Dried sections were then attached to glass slides with Accu-mount 60 mounting medium and hand polished with wet 600-grit sandpaper to a thickness of approximately 350 µm. Several staining or ring elucidation techniques (e.g. Parsons, 1983a; Branstetter, 1986; Brown and Gruber, 1988; Hoenig and Brown, 1988) failed to significantly increase increment visibility; therefore all aging was performed with unstained vertebral sections.

Vertebral sections were read on a dissecting microscope with transmitted light and a polarizing filter at 20× magnification. Increment radii and marginal increments were measured through the center of the corpus calcareum (Fig. 2) with OPTIMAS image analysis software (Media Cybernetics, 1999). Precaudal length was regressed on centrum radius (CR) for males and females to test for an isometric relationship.

The increments observed in vertebral sections were narrow circuli similar to those described by Simpfendorfer (1993), as opposed to the growth bands described by Branstetter (1987a). All increment counts were made without knowledge of the size, sex, or collection date of the specimen. The primary reader (senior author) counted increments on all samples twice; each reading was separated by at least two months. Increment counts that were not in agreement were counted a third time. If the third count did not agree with one of the first two counts, the specimen was excluded from the analysis. The secondary reader (coauthor) counted increments from all specimens not eliminated by the primary reader's analysis. Between-reader disagreements were re-examined by both observers simultaneously. All specimens for which a consensus could not be reached were discarded. The index of average percentage error (IAPE; Beamish and Fournier, 1981) was used to estimate precision between the final readings of the primary reader and the initial readings of the secondary reader

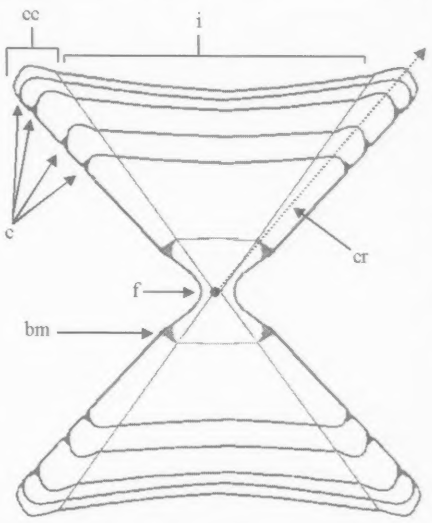

Figure 2

Diagrammatic representation of a vertebral section; bm = birth mark, c = circuli, cc = corpus calcareum, cr = line of centrum radii and annuli measurements, f = focus, i = intermedalia.

The annual periodicity of increment formation was verified through marginal increment analysis and focus-to-increment frequency distributions. Absolute marginal increment distances were converted to "relative" marginal increments by dividing the distance between the last increment and the edge of the centrum by the width of the last fully formed growth band (Skomal, 1990; Natanson, et al., 1995). This conversion compensated for differences in growth rates between age classes.

Back-calculated lengths at previous ages were estimated from vertebral measurements by using a modified Fraser-Lee equation proposed by Campana (1990):

$$L_a = L_c + [(C_a - C_c)\,(L_c - L_0)/(C_c - C_0)],$$

where L_a = length at age;
L_c = length at capture;
C_a = centrum radius from focus to increment a; and
C_c = centrum radius at capture.

L_0 and C_0 are biologically derived intercepts that represent the fish length and centrum radius, respectively, at which the proportionality between fish length and centrum growth are initiated. For the purposes of this study, mean body length and centrum radius at birth were used as the biologically derived constants (Sminkey and Musick, 1995).

The observed age-class data were used to estimate "actual ages" to 0.1 year. These were calculated by the number of circuli present plus growth since the formation of the last circulus. All specimens were given a 1 June birth date, which approximates the middle of the pupping season. This process corrected for growth since the last increment, preventing the potential overestimation of size-at-age that might result from analyzing the data by year class alone. All three types of length-at-age data (observed age class, observed actual age, and back-calculated age) were fitted to the von Bertalanffy growth equation (VBGE; von Bertalanffy, 1938):

$$L_t = L_\infty(1 - e^{-K(t - t_0)}),$$

where L_t = length at age t;
L_∞ = asymptotic length;
K = growth coefficient; and
T_0 = theoretical age at zero length.

Each of the three types were analyzed for sexes combined, as well as for each sex separately. The parameters for the VBGE were estimated through a stepwise Gauss-Newton iterative fitting process computed by JMP statistical analysis software (Anonymous, 1998).

Results

The sharpnose shark was abundant throughout the year in coastal waters within the sampling area. The ratio of males to females in the overall sample was not significantly different from a 1:1 ratio (chi-square test, n=1091, α=0.05, v=1, χ^2=1.39, P=0.24).

Linear regression of TL, NTL, and FL on PCL resulted in the following equations:

$TL = 29.804 + 1.279PCL$ (n=1009, r^2=0.99, $P<0.0001$);
$NTL = 31.678 + 1.254PCL$ (n=493, r^2=0.99, $P<0.0001$);
$FL = 11.249 + 1.075PCL$ (n=1083, r^2=0.99, $P<0.0001$).

Reproduction and maturity

Size-at-maturity estimates were based on observations of 526 males and 564 females. The smallest fully mature male was 600 mm PCL, and the largest immature male was 615 mm PCL. All males greater than 615 mm PCL and 36% of males from 600 to 615 mm PCL were fully mature. The onset and completion of maturity in male *R. terraenovae* were demonstrated by the onset of development in the claspers and siphon sac (Fig. 3). Males began to mature at 500 mm PCL. The maturation of claspers and siphon sac reached completion approximately one year later, at 600 to 615 mm PCL.

The smallest maturing female was 509 mm PCL and contained one maturing oocyte five mm in diameter. The second smallest maturing female was 529 mm PCL. The smallest gravid female was 591 mm PCL. The largest immature female, based on lack of embryos or uterine scarring, was 611 mm PCL. Females from 591 to 611 mm PCL were either gravid (63%) or contained large (>10 mm diameter) maturing oocytes and were close to their first ovulation (37%). All females greater than 611 mm PCL were mature.

Mean GSI and mean ovarian egg diameter (MOD) both demonstrated prominent peaks during the calendar year. Male GSI values were highest in April and high values were also present in March and May (Fig. 4). However, the seminal vesicles remained turgid and full of semen for some time following the seasonal testicular degeneration which began in May. Female MOD values were highest in May and June. An increase in standard error along with a drop in mean value for the month of June (Fig. 4) demonstrated that ovulation began at that time. The extremely low MOD in July indicated the completion of ovulation.

Litter sizes ranged from one to eight, and generally increased with female PCL (Fig. 5). Mean litter size was 3.85 embryos, and significantly more embryos were found in the left uterus (mean=2.19) than in the right (mean=1.65; chi-square test, n=558, α=0.05, v=4, χ^2=62.62, $P<0.0001$). Nonlinear regression of litter size on female PCL resulted in the following equation (n=278, r^2=0.51, $P<0.0001$):

$$\textit{Litter size} = -11.07 + 0.021\,PCL + 1.37 \times 10^{-4}(PCL - 710.9)^2$$

Rhizoprionodon terraenovae were born at approximately 212 mm PCL. The smallest free-swimming neonate was 190 mm PCL, and the largest full-term embryo was 242 mm PCL. Most pupping occurred from mid-May to early June. However, a small number of neonates appeared as early as mid-April. Consequently, mean embryo total length was at a minimum in July and at a maximum in June (Fig. 6). The sexes of uterine embryos were not significantly different from the expected 1:1 ratio (chi-square test, n=844, α=0.05, v=1, χ^2=0.076, P=0.78).

Age and growth

Separate linear regressions of PCL on centrum radius (CR) for males and females were not significantly different (ANCOVA, P=0.065) and were therefore combined (Fig. 7) to yield the following formula:

$PCL = 61.80 + 124.48CR$ (r^2=0.963, n=812, $P<0.0001$).

The regression line slightly overestimated centrum radius for the largest individuals (>700 mm PCL) of both sexes. Data transformation, as well as nonlinear regression, failed to increase the r^2 value, and only the largest specimens were affected.

Nonlinear regression of total body weight on length was significantly different between males and females (ANCOVA after log-transformation, $P<0.001$), and resulted in the following equations:

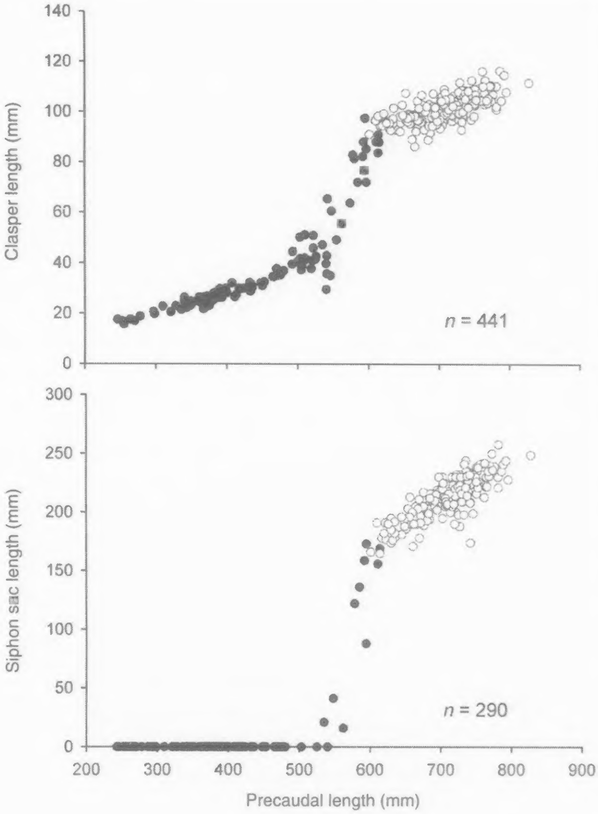

Figure 3

Relation of clasper and siphon sac length to precaudal length for male *R. terraenovae*; (●) represents individuals with uncalcified claspers; (○) represents individuals with fully calcified claspers.

Females: $W_t = e^{(-18.62)}PCL^{(3.04)}$ $(r^2=0.99, P<0.0001, n=458)$;

Males: $W_t = e^{(-18.18)}PCL^{(2.96)}$ $(r^2=0.99, P<0.0001, n=454)$,

where W_t = total body weight.

Aging was attempted on 890 specimens, 812 of which were aged without elimination. Agreement between the first and second counts conducted by the primary reader was 66%, with 91% within one increment, and 99% within two. Those sections that showed disagreement between the first and second reading (n=303) were counted a third time, and 96% agreed with one of the first two readings. The remaining 4% (12 specimens) were excluded from the analysis. Agreement between readers was 72%, with 95% within one increment and 99% within two. Vertebrae for which counts did not agree between readers (246 out of 878) were re-examined by both readers simultaneously. A concurrent age could not be reached on 66 vertebrae, which were eliminated from the study. The IAPE between the final readings of the primary reader and the initial readings of the secondary reader was 7.4%. Size-frequency distributions of the discarded individuals (data not shown) closely matched those of the raw data set and did not indicate the elimination of a large number of individuals from any age class during the aging process.

Mean relative marginal increments for age classes 1+ through 7+ combined demonstrated a minimum in July (Fig. 8). The 0+ age class was excluded from this analysis to ensure that growth from the birth mark did not affect the results. Frequency distributions of focus-to-increment measurements for ages 0+ through 7+ demonstrated single modes for all annuli in each age class for both males and females (Fig. 9).

Most *R. terraenovae* were found to have an increment in the intermedalia and an associated change in the angle of the corpus calcareum, which is similar to the birth mark described by other authors (e.g. Casey et al., 1985; Branstetter, 1987b; Simpfendorfer, 1993). There were 239 young of the year *R. terraenovae* collected during this study, 88 of which contained no discernible birth mark. All young of the year lacking a birth mark were captured in June and July (Fig. 10), whereas all young of the year captured from August through April had a birth mark. Both marked and unmarked centra were noted in July and showed a readily apparent trend; individuals with a birth mark were significantly larger than those without a birthmark (*t*-test, df=96, $t=-7.138$, $P<0.0001$).

Back-calculated lengths-at-age were similar to observed lengths-at-age in all cases, although observed values were slightly higher for all age classes (Table 1). There was no evidence of Lee's phenomenon in the older age classes. Back-calculated size at the birth mark overestimated size at birth as determined by observations of neonates and full-term embryos.

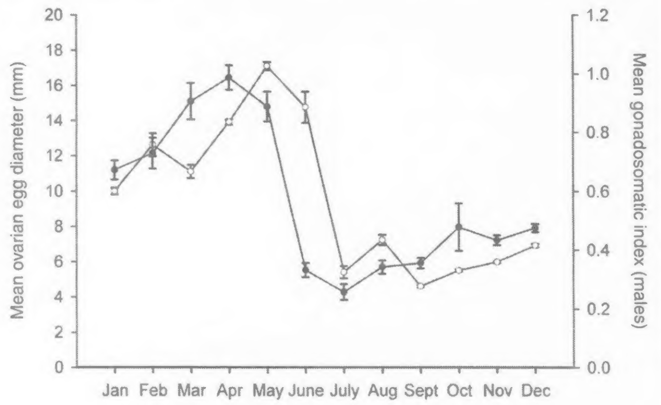

Figure 4

Mean gonadosomatic index and mean ovarian egg diameter by month for female *R. terraenovae*. Open circles indicate females (n=275), closed circles indicate males (n=214). Error bars represent mean ± one standard error.

The VBGE estimates calculated by age class, actual age, and back-calculated age demonstrated little variation either within or among data types (Table 2). The VBGE parameters from all data types corresponded well with known life history parameters for size at birth and maximum size. Unless otherwise noted, all comparisons throughout the remainder of this study were based on VBGE estimates derived from the "actual age" data type.

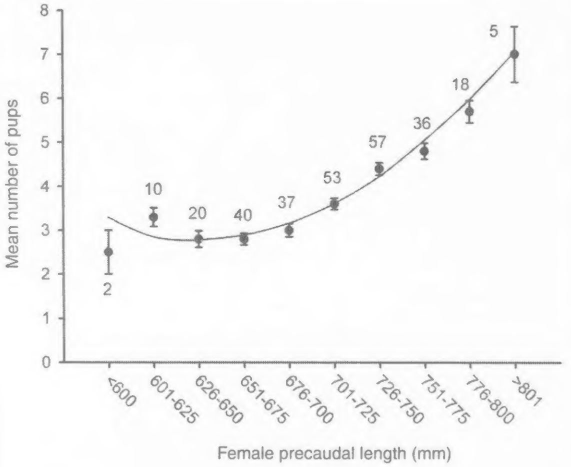

Figure 5

Mean litter size on female size class. Solid line represents best-fit quadratic equation. Numbers indicate sample size for each data point. Error bars represent mean ± one standard error.

Discussion

Reproduction

Length-at-maturity estimates for male *R. terraenovae* were similar among the three published studies. Parsons (1983b) estimated male maturity at ~610 to 653 mm PCL (lengths from other studies were converted to PCL by using the formulae derived from the current study) and Branstetter (1987a) estimated the same at 600 mm PCL. We determined that males reach full maturity at ~600 to 615 mm PCL. The three studies failed to agree on length at maturity for female *R. terraenovae*. Branstetter (1987a) and Parsons (1983b) approximated the size of females at maturity at 660 mm PCL and from 650 to 690 mm PCL, respectively. We found, however, that females mature at a smaller size, from 590 to 610 mm PCL.

The reproductive seasonality of *R. terraenovae* in our study appeared to lack synchrony; males reached their reproductive peak in April and females in May and June. Mature males dissected in late May and June had visibly atrophied testes compared to those collected in April and early May. However, their seminal vesicles were still highly swollen and contained large amounts of semen. This condition indicated that male *R. terraenovae* were still capable of mating during May and June, when female MOD values were highest. Therefore, the mating season of *R. terraenovae* off the southeastern U.S. coast appeared to last from mid May to early July. Simpfendorfer (1992) noted a similar misalignment of peaks in reproductive seasonality between the sexes in *R. taylori*.

The largest litters noted in our study contained eight pups (n=4). This increases the maximum litter size reported for *R. terraenovae* in the northwestern Atlantic

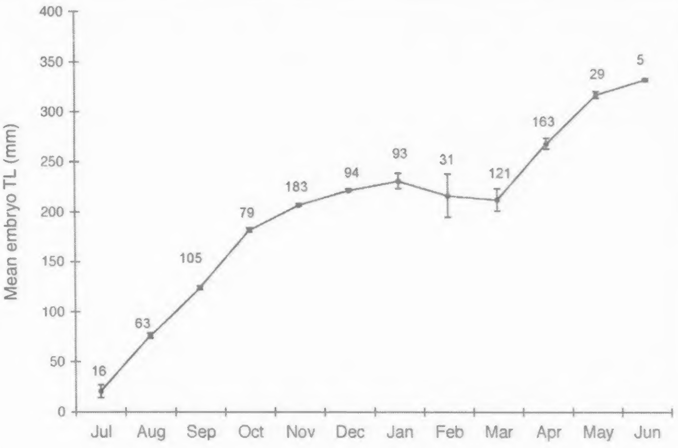

Figure 6

Mean total length by month for embryos collected from April 1997 through March 1999. Numbers indicate sample size for each data point. Error bars represent mean ± one standard error.

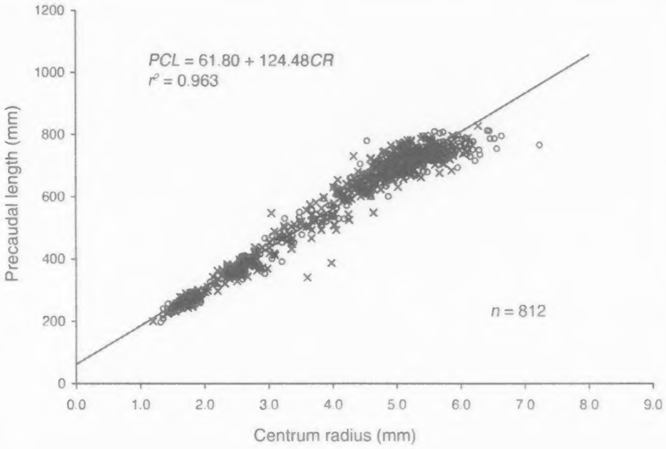

Figure 7

Linear regression of precaudal length (mm) on centrum radius (mm) for *R. terraenovae*; (X) represents males, (O) represents females.

(Parsons, 1983b; Castro and Wourms, 1993). Early reports of up to 12 pups in sharpnose sharks collected from Cuban waters (Bigelow and Schroeder, 1948) were likely the result of misidentification (Castro and Wourms, 1993).

Age and growth

The PCL-CR regression line slightly overestimated centrum radius for large individuals. This trend has also been noted in large female *Carcharhinus obscurus* (Natanson et al., 1995) and appears to result from a change in the slope of the linear relationship as growth becomes asymptotic near the maximum length of the species. This phenomenon was deemed to have a minimal effect on the linear regression formula used in this study. Although the linear relationship appears to undergo an immediate change in slope at about 700 mm PCL, there are not enough data following this change (that is, the animal does not increase substan-

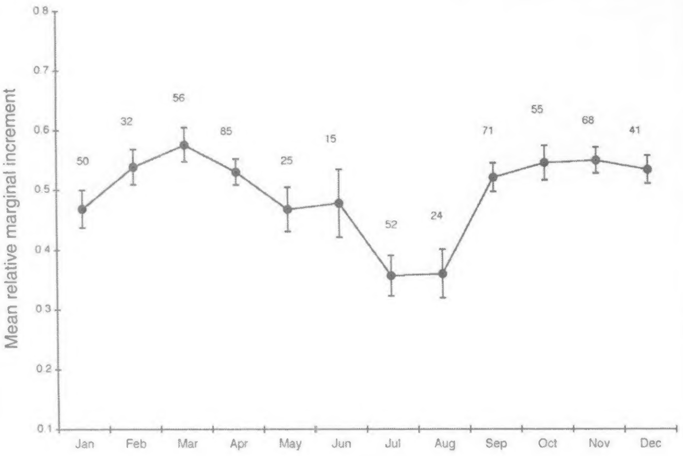

Figure 8

Mean relative marginal increment (mm) by month for age classes 1+ through 7+. Numbers indicate sample size for each data point. Error bars represent mean ± one standard error.

Table 1

Mean, minimum, and maximum lengths-at-age (mm) and statistics for observed actual and back-calculated ages (0–10+ years).

	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+
Females											
Back-calculated											
mean	249	452	556	619	665	698	722	740	754	775	777.9
minimum	189	307	422	521	563	600	627	673	711	754	
maximum	301	573	646	742	764	795	795	800	785	804	
SD	19	32	35	36	35	34	29	28	22	19	
n	379	305	273	232	186	137	90	42	13	5	1
Observed											
mean	320	513	629	676	700	717	741	755	762	788	787.0
minimum	197	391	469	606	615	345	663	688	726	764	
maximum	465	624	707	780	765	805	812	810	796	813	
SD	63	51	49	33	30	66	26	31	23	20	
n	123	32	42	46	50	47	48	29	8	4	1
Males											
Back-calculated											
mean	247	452	564	634	675	695	708	717	728	715	
minimum	191	310	372	519	582	625	651	690	706		
maximum	317	553	681	760	778	809	753	764	743		
SD	21	36	45	40	38	32	24	21	16		
n	337	260	225	191	159	102	49	15	4	1	
Observed											
mean	323	509	600	676	716	722	722	732	743	720	
minimum	200	340	387	578	623	653	661	699	729		
maximum	466	602	730	777	796	828	763	773	757		
SD	63	59	69	46	39	34	24	21	14		
n	116	35	34	32	57	53	35	10	3	1	

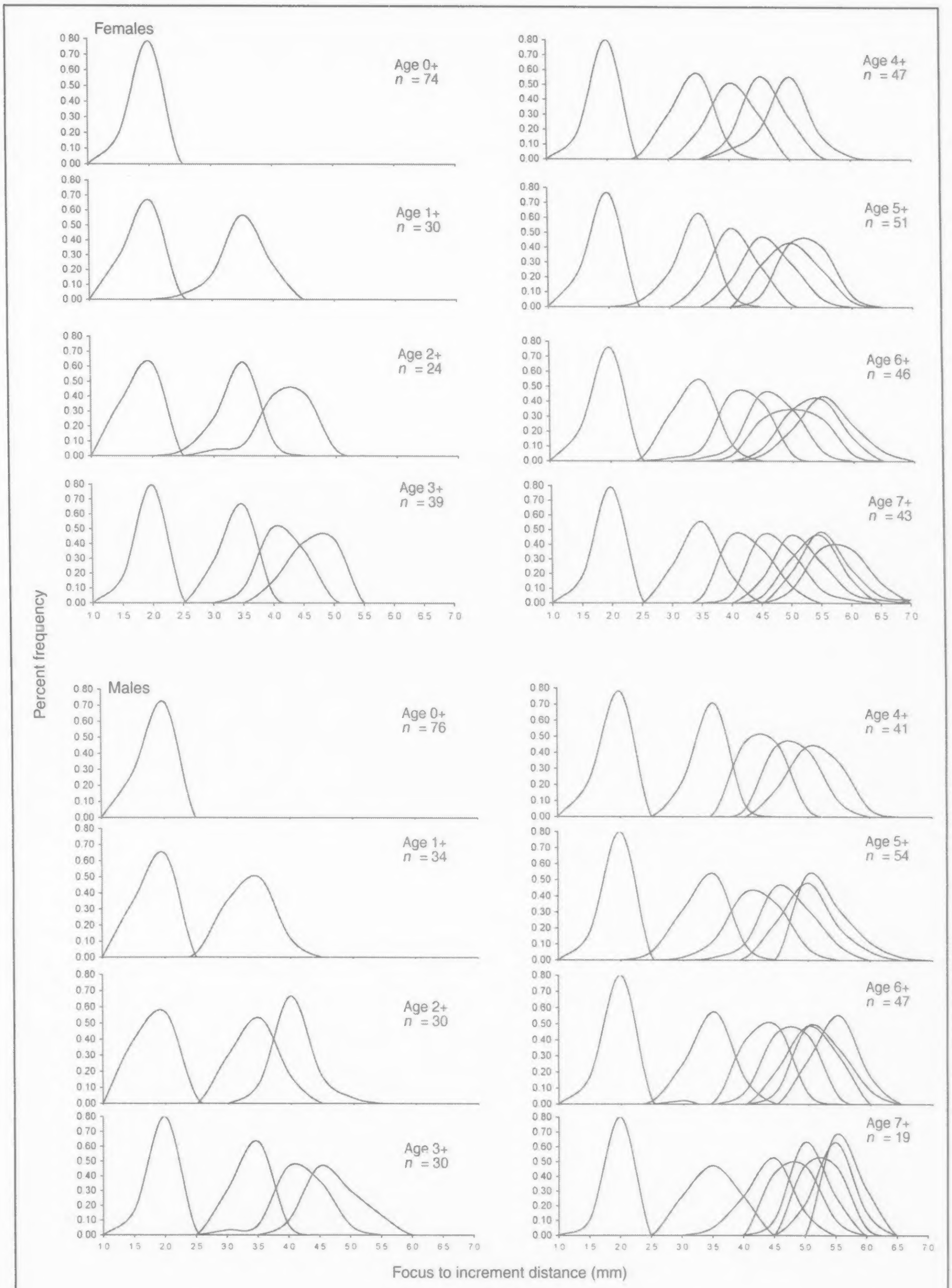

Figure 9

Focus to increment distance (mm) frequency distributions for males and females age 1+ to 7+. The first distribution represents the birth mark in all cases, subsequent distributions represent (from left to right) measurements to the first, second, third, fourth, fifth, sixth, and seventh increments, respectively.

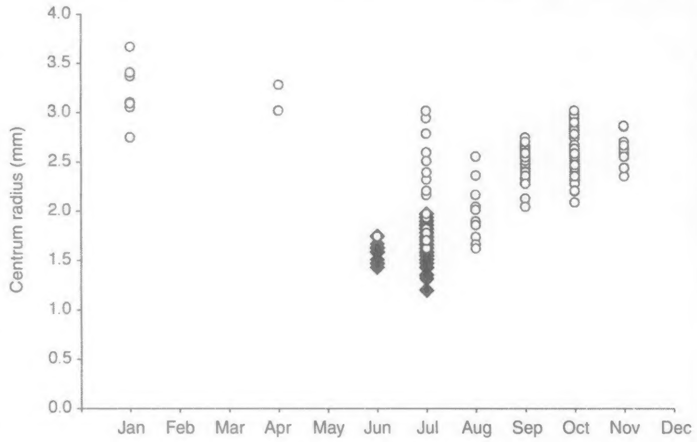

Figure 10

Centrum radius of age 0+ *R. terraenovae*, by month. (♦) represents individuals without a birth mark, (○) represents individuals with a birth mark.

Table 2

Von Bertalanffy growth parameters of *Rhizoprionodon terrraenovae* from the southeastern coast of the United States. Von Bertalanffy growth parameters from previous studies in the northern Gulf of Mexico are included for comparison.

	Von Bertanalanffy growth parameters								
Sex	L_∞ (mm PCL)	K	t_0	SE of L_∞	SE of K	SE of t_0	n	Data type	Study
Females	752	0.52	–1.07	5.33	0.025	0.052	433	age class	current
Males	746	0.53	–1.07	6.83	0.030	0.059	379		
Sexes combined	750	0.52	–1.07	4.23	0.019	0.039	812		
Females	749	0.49	–0.94	4.60	0.020	0.046	433	estimated actual age	current
Males	745	0.50	–0.91	5.93	0.024	0.052	379		
Sexes combined	748	0.50	–0.92	3.65	0.015	0.034	812		
Females	738	0.46	–0.90	2.64	0.006	0.015	1856	back-calculation	current
Males	726	0.53	–0.79	3.14	0.009	0.016	1447		
Sexes combined	732	0.49	–0.85	2.02	0.006	0.011	3303		
Sexes combined	820	0.36	–0.99	—	—	—	20	estimated actual age	Branstetter (1987a)
Males	709	0.39 to 0.53	–2.01	—	—	—	15	age class	Parsons(1985)

tially in length following the shift) to reliably fit a second regression line. The back-calculation equation used in our study does not employ the linear regression in its calculations and was minimally affected by the negative bias that this phenomenon had on the slope of the regression.

Marginal increment analysis in the present study indicated that growth increments form in summer. This finding is contrary to that of earlier studies on *R. terraenovae*, which indicated winter deposition (Parsons, 1985; Branstetter and McEachran, 1986; Branstetter 1987a). However, other species in this genus have been shown to deposit increments during the summer months. Simpfendorfer (1993) demonstrated summer (February) increment deposition in *R. taylori* in Australian waters. He cited stress during the breeding season as a possible cause because hepatosomatic index and condition factor in both sexes were low during the mating season, an indication of probable stress. Furthermore, growth increments in elasmobranchs may reflect periods of slow calcareous accretion that have been compressed by increased growth (Gelsleichter, 1998). This pattern of deposition may result in increments from periods of slow growth not becoming

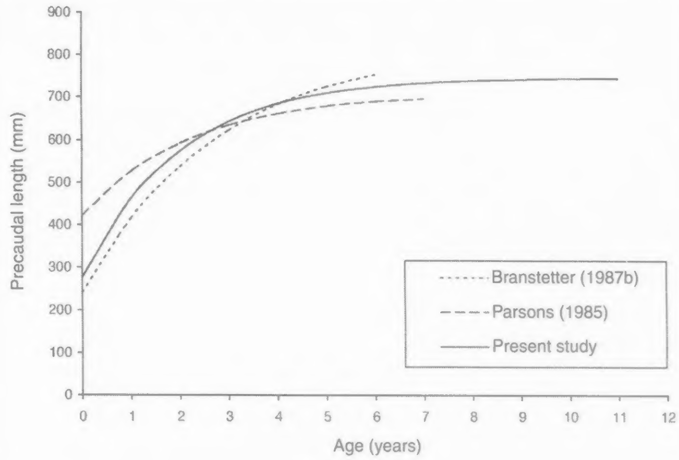

Figure 11

A comparison of growth curves for *R. terraenovae* from the present study with those from previous works by other authors. Growth curve from the present study is based on estimated actual ages for both sexes (parameter values are presented in Table 2).

visible for some time after their actual formation until enough new tissue has grown distally to provide the compression and contrast necessary for reliable identification. In other words, the increments observed in our study first became visible in July, but may have actually formed one to several months earlier. It should be noted that the methods of vertebrae processing and examination followed during our study were more similar to those of Simpfendorfer (1993) than to those of Parsons (1985) or Branstetter (1987a). These methods may have contributed to the close similarity found in both the physical appearance (i.e. that of "check marks" as opposed to pairs of growth bands) and temporal deposition of increments between our study and that of Simpfendorfer (1993).

We found young of the year *R. terraenovae* with and without a birth mark. This is unusual in that most studies that have documented the presence of a birth mark have found one present in all specimens examined (e.g. Casey et al., 1985; Branstetter, 1987b; Simpfendorfer, 1993). Simpfendorfer (1993) suggested that the "birth" mark in *R. taylori* was probably laid down sometime after birth because he observed the same overestimation of size at birth by back-calculations noted previously in our study. No temporal estimation of the lag between birth and the formation of a birth mark has been published. The young-of-the-year *R. terraenovae* examined during our study demonstrated a distinct temporal transition from the lack of a birth mark to the presence of a birth mark (Fig. 10). The data suggest that the birth mark is not actually laid down at birth in June, but approximately one month later in July. This time lag may explain the overestimation of size at birth by back-calculation. It is possible that the mechanism for the formation of the birth mark lies in the switch from embryonic to normal somatic growth, which may not occur immediately following parturition.

The von Bertalanffy growth parameters derived for our study demonstrated differences from those derived for previous studies (Fig. 11). Parsons (1985) estimated an L_∞ of 709 mm PCL, and Branstetter (1987a) 820 mm PCL. L_∞ for our study was 745 mm PCL for males, and 749 mm PCL for females. The t_0 value produced by Parsons was low at –2.01 yr, whereas the values produced by Branstetter (–0.99 yr) and our study (–0.90 yr for males and –0.94 yr for females) agreed well with the known gestation period of approximately 11 months. Parsons (1985) estimated K by several methods, resulting in values ranging from 0.39 to 0.53. The higher values agreed well with the estimates of our study (0.49 for females and 0.50 for males). Branstetter's (1987a) estimate of K was 0.36, lower than that of the current study.

Yearly growth rate estimates by Parsons (1983b) and Branstetter (1987a) revealed an increase of 133 to 211 mm PCL during the first year of life, 94 mm during the second year, 55 mm during the third year, and 16 to 32 mm growth after maturity. We found similar, though slightly higher growth rates: 198 to 202 mm PCL during the first year, 100 to 108 mm during the second, 63 to 69 mm during the third, and from 0 to 46 mm thereafter.

Parsons (1985) determined age at maturity by three methods: extrapolation of growth rates to size at maturity, the VBGE, and Holden's method (Holden, 1974). The estimates produced by these methods ranged from 2.0 to 3.5 for males, and 2.4 to 3.9 for females. Branstetter (1987a) compared his von Bertalanffy-derived estimates to those of Parsons (1985), and found his results in general agreement with Parsons' higher estimates. Branstetter (1987a) thus concluded that males mature in three years and females in four. In our study, males reached full maturity at 2.4 to 2.6 years of age, making them functionally mature at the third breeding season following birth. Females were found to mature at 2.2 to 2.5 years, which would also result in full maturity just prior to the third postnatal breeding season. Although it was noted in both previously cited studies that males matured six months to one year earlier than females, no such discrepancy in age at maturity between the sexes was apparent in our study.

Differences between studies

The differences between this and previous studies on *R. terraenovae* are likely a combination of many contributing factors. These studies were conducted in different regions at separate times and may reflect clinal or temporal differences (or both) between Gulf of Mexico and northwestern Atlantic *R. terraenovae* populations. However, there are other contributing factors that must be considered as well, most notably differences in data collection and analysis techniques.

Parsons' (1985) growth curves were based on males and were grouped into age classes (not assigned actual ages). His von Bertalanffy parameters were then derived by using the Ford and Walford plot method (Parsons, 1985), requiring the use of mean lengths of each age class. This age class grouping does not take into account growth since the deposition of the last increment, and may therefore bias the Ford and Walford plot by pulling the data to a faster asymptote (Branstetter and McEachran, 1986; Branstetter, 1987a;). This bias produced a low L_∞ (706 mm PCL) and t_0 (–2.01 years) in Parsons' estimates (Branstetter and McEachran, 1986; Branstetter, 1987a). This phenomenon was not evident in VBGE estimates based on age classes in our study, which were very similar to estimates based on actual ages (Table 2), and was probably due to the fact that iterative fitting of age data to the VBGE by computer software (an option unavailable to Parsons at the time of his study) is less sensitive to unaddressed growth than the graphically based Ford and Walford plot method.

Although the aging technique used by Branstetter (1987a) was similar to that of our study (counts on longitudinal sections of cervical centra), Parsons' (1985) aging technique took ring counts from the face of centra that had been removed from a more posterior region of the vertebral column than the region chosen in our study. It has been stated by several authors (Branstetter and McEachran, 1986; Martin and Cailliet, 1988; Kusher et al., 1992) that increment counts made from sections of vertebral centra are generally preferable to those taken from the face of unsectioned centra. Sectioned centra allow for better documentation of the increment structure near the edge because the increments become narrower and more difficult to delineate with increasing age (Branstetter and McEachran, 1986; Martin and Cailliet, 1988; Kusher et al., 1992). This distinction is critical when the potential consequences of age underestimation (including overestimation of *K*, growth rate, and maximum sustainable yield) are considered.

Based on comparison of our work to that of previous studies (Branstetter, 1981, 1987a; Parsons, 1983a, 1983b, 1985), there may be differences between the Gulf of Mexico and southeastern U.S. Atlantic populations of Atlantic sharpnose sharks. The question then becomes whether these differences are clinal or temporal in nature. Clinal variation, for instance, may explain the differences noted in size and age at maturity in female *R. terraenovae*. Simpfendorfer (1993) noted differences in size at maturity between populations of *R. taylori* in Australia, as did Parsons (1993) and Carlson et al. (1999) between populations of *Sphyrna tiburo* and *Carcharhinus acronotus*, respectively, off the Gulf coast of Florida. However, the extended time frame between the current and previous studies (15 to 20 years), also opens the possibility that the differences are related to a temporal change in population structure of the species across the entire Gulf and Western Atlantic region. In the earlier studies, data were collected during a time when fishing pressure (both directed and indirected) on *R. terraenovae* was lower than at present, and fisheries were shown to have dramatic effects on shark populations in less time (Anonymous[1]). The differences noted between the studies may thus be a manifestation of temporal changes in population structure of the species as a whole over the last two decades. A more current study on Gulf of Mexico *R. terraenovae* is needed to properly address these potential population differences.

Conclusion

Small shark species such as *R. terraenovae* tend to show rapid growth in the first few years of life and a dramatically slower growth rate once maturity is reached. This aspect of their growth complicates age estimation by vertebral increments because the most recent marks in older specimens are so closely spaced that accurate counting and measurement become problematic. The overlapping of increments in these older specimens or the lack of identifiable increment formation altogether due to asymptotic growth may lead to an underestimation of ages in large adults. Althhough the maximum age demonstrated in our study was 11+ years, the actual life span of *R. terraenovae* may be longer.

The life history parameter estimates that have been presented in our study are based on one of the largest short-term samples collected for any study of elasmobranch life history to date. The most significant aspect of this study is the documentation of differences in size and age at maturity between female *R. terraenovae* in the Gulf of Mexico and females off the southeastern U.S. coast. A difference in age of maturity of one year in an animal with a relatively short life span, such as *R. terraenovae,* can have a dramatic effect on the outcome of population models (see Cortes, 1995). Although the documentation of age at maturity differences by different researchers may be highly susceptible to analytical bias during the aging process, the documentation of differences in size at maturity is unmistakable.

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[1] Anonymous. 1993. Fishery management plan for sharks of the Atlantic Ocean, 167 p. U.S. Dep. Commerce., NOAA, NMFS, Silver Spring, MD 20910.

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Abstract—We present a method to integrate environmental time series into stock assessment models and to test the significance of correlations between population processes and the environmental time series. Parameters that relate the environmental time series to population processes are included in the stock assessment model, and likelihood ratio tests are used to determine if the parameters improve the fit to the data significantly. Two approaches are considered to integrate the environmental relationship. In the environmental model, the population dynamics process (e.g. recruitment) is proportional to the environmental variable, whereas in the environmental model with process error it is proportional to the environmental variable, but the model allows an additional temporal variation (process error) constrained by a log-normal distribution. The methods are tested by using simulation analysis and compared to the traditional method of correlating model estimates with environmental variables outside the estimation procedure. In the traditional method, the estimates of recruitment were provided by a model that allowed the recruitment only to have a temporal variation constrained by a log-normal distribution. We illustrate the methods by applying them to test the statistical significance of the correlation between sea-surface temperature (SST) and recruitment to the snapper (*Pagrus auratus*) stock in the Hauraki Gulf–Bay of Plenty, New Zealand. Simulation analyses indicated that the integrated approach with additional process error is superior to the traditional method of correlating model estimates with environmental variables outside the estimation procedure. The results suggest that, for the snapper stock, recruitment is positively correlated with SST at the time of spawning.

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A general framework for integrating environmental time series into stock assessment models: model description, simulation testing, and example

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Identifying a clear relationship between an environmental variable and processes in the dynamics of the population (recruitment, natural mortality, growth) or the fishery (catchability) would allow improved estimation and prediction of model parameters and derived quantities. It is well known that the environment plays a large role in the population dynamics and catchability of fish stocks. Many researchers (Green, 1967; Joseph and Miller, 1989; Hinton and Nakano, 1996; Lehodey et al., 1997; Shepherd et al., 1984) have identified correlations between population processes and environmental factors, and others (Hunter, 1983; Bertignac et al., 1998; Lehodey et al., 1998) have suggested hypotheses for the underlying causes of these correlations. Incorporation of environmental time series into stock assessment models may provide additional information to help estimate model parameters, particularly when fishing observations (catch, effort, length-frequencies) are missing. For the management of fish stocks, it can be advantageous to be able to predict future catch rates and population sizes. Because there is often a delay due to the propagation of the recruitment signal in the population structure or because statistical and numerical models can provide predictions for some environmental variables (e.g. temperature) (or for both reasons), the relationship can be used to predict future catch rates or population sizes.

Statistical catch-at-age analysis (e.g. Fournier and Archibald, 1982; Deriso et al., 1985; Methot, 1990) is more appropriate than cohort analysis (virtual population analysis) to include relationships between an environmental variable and processes in the dynamics of the population. In cohort analysis, if there are missing data, they are simply extrapolated without any statistical methods, which may cause bias in the parameter estimates. Also, the potential correlation with an environmental series is calculated outside of the estimation procedure, producing several disadvantages, including the loss of information and the difficulty of propagating uncertainty (Maunder, 1998a, 2001a, 2001b). However, in statistical catch-at-age analysis, there are robust statistical methods (maximum likelihood, with all the parameters estimated together by obtaining the best fit between predicted and observed data) that allow inclusion of multiple data sets and the integration of the environmental series into the stock assessment model. These methods automatically allow for missing data and provide confidence intervals, and the hypotheses can be easily incorporated and tested.

The methods used to integrate the environmental series into the stock assessment model can be applied to different processes in the population, but are illustrated here with the case of recruitment. Recruitment is the fundamental process in the population dynamic that is responsible for the fluctuations of the stock size. Many studies (e.g. Francis, 1993) show that environmental variables affect the recruitment. In statistical catch-at-age analysis, recruitment combines an average value with an annual deviate, constrained by using a distributional assumption (e.g. Maunder and Starr, 2001). This constraint allows the estimation when there is no information (i.e. missing data). Traditional methods that relate recruitment to environmental factors use correlation analysis of an environmental time series with estimates of recruitment from a stock assessment model. For example, cohort analysis is first used to generate a time series of recruitment. Then the time series of recruitment is regressed against sea-surface temperature (SST). This two-step procedure has a number of disadvantages (Maunder, 1998a, 2001a, 2001b), including the loss of information and the difficulty of propagating uncertainty.

We introduce a method suggested by Maunder (1998a; see Maunder and Starr, 2001) that incorporates environmental time series into stock assessment models and tests the significance of the correlation between the population processes and the environmental time series. We test the model with simulated data and compare the results to correlating model estimates with environmental variables outside the estimation procedure. We illustrate this method with an application that investigates the correlation between SST and recruitment within the context of a statistical catch-at-age analyses used to assess snapper (*Pagrus auratus*) in the Hauraki Gulf–Bay of Plenty, New Zealand (Maunder and Starr, 2001).

Materials and methods

Integrating environmental indices into stock assessment models

Parameters that relate the environmental time series to population processes were included in the statistical catch-at-age stock assessment model. We added additional structure to the stock assessment model for each parameter of the stock assessment model (X) that was hypothesized to 1) have temporal variation, 2) be correlated with an environmental time series, and 3) have sufficient information in the data to be estimated for multiple time periods. This structure included a mean value for the stock assessment model parameter (μ), temporal deviations in the stock assessment model parameter (ε_t), a parameter that relates the environmental series to the stock assessment model parameter (β), and a scaling parameter (α) that ensures that μ is the mean value for the stock assessment model parameter over the time period used in the model.

$$X_t = \mu \exp(\alpha + \beta I_t + \varepsilon_t), \qquad (1)$$

where t = time, and
I_t = the value of the environmental time series at time t.

The parameter α ensures that μ is equal to the mean over the whole time period (Gilbert[1]; see Maunder and Starr, 2001). Therefore, α removes the log normal bias and bias caused by an unnormalized environmental time series and is defined as

$$\alpha = \ln\left(\frac{n}{\sum \exp(\varepsilon_t + \beta I_t)}\right), \qquad (2)$$

where n is the number of time periods.

The additional structure requires that a set of parameters (ε_t) that are constrained by a distributional assumption and two free parameters (μ, β) be estimated. The distributional assumption (referred to as a "prior" in the following description and represented by the negative logarithm of the prior probability, see Eq. 3) is a prior on the degree of temporal variation in the stock assessment model parameter. The default assumption is a normal distribution (assuming that the stock assessment model parameter is lognormally distributed) with mean zero and given standard deviation. Information about this distribution can be obtained from estimates for similar species (e.g. Myers et al., 1995). The prior

$$-\ln \text{Prior}\,(\varepsilon \mid \sigma) = \sum_t \frac{(\varepsilon_t)^2}{2\sigma^2} \qquad (3)$$

keeps the temporal deviations close to zero if there is no information in the data to the contrary. It is important to note that the prior is also needed to avoid making β a redundant parameter.

The parameters μ and β and the set of parameters ε_t are estimated simultaneously with the other parameters of the stock assessment model, and the negative logarithm of the prior is added to the negative log-likelihood function of the stock assessment model. The parameter estimates are really the mode of the posterior distribution, but we treat them in a likelihood context. The influence of the environmental time series can be removed from the analysis by fixing β at zero. Therefore, likelihood ratio tests can be used to determine if the β parameter significantly improves the fit to the data. If the addition of β reduces the total negative log likelihood by more than about 1.92 units ($\chi^2_{1,\alpha=0.05}$), then the additional parameter significantly improves the fit to the data at the 0.05 level, and there is a statistically significant correlation between the population process and the environmental time series. Similar tests can be performed to test the significance of the set of temporal deviation parameters, ε_t, by taking into account the number of additional parameters. Hilborn and Mangel (1997) provided a simple description of the likelihood ratio test. (The Akaike information criterion or the Bayes information criterion could also be used.) Therefore, by fixing, or not, β or ε at zero we can define three types of statistical models:

1 Traditional model
β is fixed at zero, the parameter set ε_t is estimated, and a significant relationship is determined by testing if the correlation coefficient between ε_t and the environmental time series is significantly different from zero.

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[1] Gilbert, D. J. 1999. Personal commun. National Institute of Water and Atmospheric Research Limited, P.O. Box 14-901, Wellington, New Zealand.

2 Environmental model
β is estimated, each value in the parameter set ε_t is fixed at zero, and a significant relationship is determined by testing if $\beta = 0$, using a likelihood ratio test.

3 Environmental model with process error
Both β and ε_t are estimated and a significant relationship is determined by testing if $\beta = 0$, with a likelihood ratio test.

Simulation testing

Simulation analysis was carried out to test the performance of the integrated approach and to compare this approach to the traditional model. A simple age-structured model (Appendix I) was set up to simulate a population for 20 years, starting from an unexploited population and generating catch, effort, and catch-at-age data. The simulated recruitment was generated as having a component based on an environmental time series and a random component. Each component was given the same variance (0.6^2). The environmental time series was randomly generated with $\beta = 1$ for each simulation. The standard deviation of the observation error in the CPUE index, σ_{CPUE}, was set at 0.6, and the sample size of the catch-at-age data was set to 50. The same age-structured model was then fitted to the data to estimate the model parameters. The three models defined in the previous section (traditional model, environmental model, and environmental model with process error) were tested with the simulated data. In addition to the parameters outlined in the description of the three models, average recruitment, the catchability coefficient, and the standard deviation of the fit to the CPUE data were also estimated. We also used a model that had constant recruitment to provide likelihood values to use in testing the significance of the environmental model.

The simulation analysis was repeated 500 times for four scenarios: 1) using catch-at-age data for all years, 2) using catch-at-age data for the first 10 years, 3) using catch-at-age data for the last 10 years, 4) using catch-at-age data for all years, but using $\beta = 0$ when generating the simulated data. Scenario 4 was used to investigate the probability of type-I error of the models when used in combination with the statistical tests. For each set of simulated data and each model, we determine how often a significant relationship between the logarithm of annual recruitment and the environmental time series is detected, the estimate of the slope of the relationship between the logarithm of annual recruitment and the environmental time series, the estimates of average recruitment, and the depletion level (ratio of current to unexploited biomass). We also calculate minimum-width 95% confidence intervals for average recruitment, using the likelihood profile method for the simulated data sets with catch-at-age data for all years.

Application: relating recruitment in the Hauraki Gulf–Bay of Plenty snapper stock to SST

Recruitment to the Hauraki Gulf snapper (*Pagrus auratus*) stock is correlated with temperature (Paul, 1976). The abundance of 1+ snapper in the Hauraki Gulf estimated by trawl surveys has been shown to have a positive correlation with SST (Francis, 1993) and air temperature (Gilbert, 1994) around or just after the time of spawning in the previous year. This relationship has also been shown with catch-at-age analysis to continue to hold as snapper enter the fishery at ages 4 and older (Maunder and Starr, 1998).

We applied the integrated approach described in this study in combination with the age-structured statistical catch-at-age model described in Maunder and Starr (2001) to the Hauraki Gulf–Bay of Plenty snapper stock. The model was fitted to catch-at-age data and biomass estimates. The biomass estimates were available for 1985 and 1994 and were obtained from analysis of tagging data. The majority of the catch-at-age data were available from 1990 to 1997, but there were some catch-at-age data of dubious quality, small sample size, and high variability for 1970 to 1973. The annual recruitment at age 1 was estimated for the time period of the model (1970–98) and also for 18 age classes (ages 2 to 19) that comprised the initial conditions in 1970.

Results

Simulation analysis

For all four sets of simulated data the environmental model had the highest probability of detecting a relationship between recruitment and the environmental time series (Table 1). This model had a very high probability of detecting a relationship even when there was no relationship in the simulated data (Table 1D). This indicates that the likelihood ratio test is not appropriate for the environmental model (see Appendix III). For all data sets, except that with only catch-at-age data in the first 10 years, the traditional model had a higher probability of detecting a relationship between recruitment and the environmental time series than did the environmental model with process error. The environmental model with process error had a lower probability of detecting a true relationship than the traditional model, but also had a slightly lower probability of type-I error (the probability of incorrectly accepting a nonexistent relationship) than the traditional model. The probability of detecting a relationship was reduced as the number of catch-at-age data sets was reduced.

The environmental model with process error did not show any bias in the estimate of the slope of the relationship between the logarithm of annual recruitment and the environmental time series, β (Table 1). For this model, the variation in the estimates of β increased when fewer years with catch-at-age data were available. The environmental model showed a small negative bias and slightly more error in the estimates of β. The traditional model showed a large negative bias in the estimate of the slope of the relationship between the logarithm of annual recruitment and the environmental time series, and this bias increased as the amount of catch-at-age data was reduced. The traditional method also had larger error, which increased as less catch-at-age data were available.

The errors in the estimates of average recruitment and B_{cur}/B_0 increased slightly with less catch-at-age data

Table 1

(**A**) Results from the simulation analysis in which all the catch-at-age data were used. % = percentage of data sets that produced a significant relationship between the environmental time series and recruitment; β = average (average absolute relative error) of the estimates of the slope of the relationship between the environmental time series and recruitment; R_0 = average (average absolute relative error) of the estimates of the average recruitment; B_{cur}/B_0 = average error (average absolute relative error) in the estimate of the ratio of current to unexploited biomass. β was set to 1 when generating the simulated data. (**B**) Results from the simulation analysis using only the first 10 years of catch-at-age data. β was set to 1 when generating the simulated data. (**C**) Results from the simulation analysis using only the last 10 years of catch-at-age data. β was set to 1 when generating the simulated data. (**D**) Results from the simulation analysis using all the catch-at-age data, but setting $\beta = 0$ when generating the simulated data. (Absolute, rather than relative, error was used for β.) EMwPE = environmental model with process error.

	%	β	R_0	B_{cur}/B_0
A				
Traditional	92	0.86 (0.25)	996 (0.05)	–0.01 (0.15)
Environmental	99	0.95 (0.25)	1,024 (0.10)	0.03 (0.24)
EMwPE	83	1.01 (0.23)	988 (0.05)	–0.04 (0.14)
B				
Traditional	57	0.45 (0.55)	1,011 (0.07)	–0.03 (0.17)
Environmental	95	0.94 (0.33)	1,078 (0.17)	0.01 (0.27)
EMwPE	60	1.05 (0.30)	1,004 (0.07)	–0.03 (0.15)
C				
Traditional	81	0.68 (0.36)	1,022 (0.09)	0.04 (0.21)
Environmental	97	0.95 (0.32)	1,035 (0.10)	0.04 (0.25)
EMwPE	74	1.00 (0.26)	1,007 (0.08)	–0.02 (0.19)
D				
Traditional	3	–0.01 (0.20)	1,005 (0.04)	0.01 (0.10)
Environmental	61	–0.02 (0.22)	1,038 (0.09)	0.07 (0.21)
EMwPE	2	–0.01 (0.21)	1,003 (0.04)	0.01 (0.10)

Table 2

Results related to the confidence intervals for average recruitment from the simulation analysis obtained by using all the catch-at-age data. EMwPE = Environmental model with process error.

	Lower bound average	Upper bound average	Lower bound SD	Upper bound SD	True is within	True is below	True is above
Traditional	888	1,120	59	132	0.91	0.03	0.08
Environmental	963	1,117	94	176	0.44	0.32	0.24
EMwPE	887	1,118	56	120	0.92	0.01	0.07

(Table 1). The errors in these estimates were slightly greater for the environmental model (more bias and larger absolute error) than for the environmental model with process error and traditional model.

The confidence intervals on R_0 were, on average, greater for the traditional and environmental model with process error than for to the environmental model (Table 2), which greatly underestimated the width of the confidence intervals. However, the confidence intervals for the traditional and environmental model with process error showed the true value falling below the confidence interval less often than it fell above it.

As expected, an environmental relationship was more difficult to correctly detect with the traditional model in situations with missing data (e.g. when catch-at-age data were missing in the last few years of the series), and, as stated above, using the environmental model is inappropriate because it has a high probability of detecting a significant relationship when none exists. The environmental model also has a tendency to under estimate the width of the confidence interval for R_0 and the true value frequently falls outside of this confidence interval. Therefore, the environmental model with process error is the model of choice.

Application: relating recruitment in the Hauraki Gulf–Bay of Plenty snapper stock to SST

The environmental model with process error has the lowest negative log-likelihood, but this model has many more parameters than the environmental model (Table 3).

Table 3

Results from applying the three methods (traditional, environmental, and environmental with process error) to the snapper application. Constant = recruitment is constant each year and equal to the average recruitment. EMwPE = environmental model with process error. n/a = not applicable.

	Average recruitment	β	–ln(Likelihood)	Number of parameters
Constant	13,315 (11,381–15,381)	n/a	482.5	3
Traditional	11,406 (8,500–14,603)	0.20	466.8	50
Environmental	13,530 (11,527–15,569)	0.48	473.5	4
EMwPE	12,029 (9,147–15,328)	0.55	464.4	51

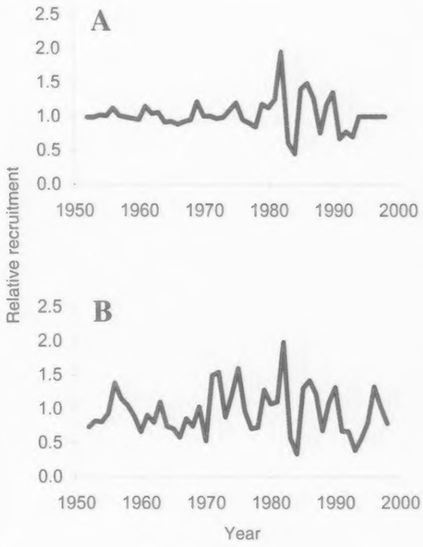

Figure 1

Annual estimates of relative recruitment strength at age 1 for the Hauraki Gulf–Bay of Plenty snapper stock from the traditional (**A**) and environmental model with process error (**B**) models

Using the likelihood ratio test at the 0.05 level and compensating for the difference in the number of parameters being estimated in each model, we consider the environmental model to be the model of choice. If the likelihood ratio test were used, the environmental model with process error would be chosen over the traditional model, indicating a statistically significant correlation between SST and recruitment. Due to the weaknesses of the environmental model discussed above, we concentrated on the results of the traditional model and the environmental model with process error.

The time series of estimated recruitments from the traditional model showed very little annual variation in recruitment for the first half of the time series and for the last few years of the time series (Fig. 1A). This indicates that there is very little information in the data (catch-at-age) about annual recruitment for these time periods and that the prior on the recruitment residuals constrains the estimated recruitment to be close to the average recruitment. This result is consistent with the catch-at-age data, which, ignoring the inconsistent data from the 1970s, started in 1990. The greatest age in the catch-at-age data that had individual information was age 19; therefore the 1971 cohort is the first for which there is information. However, at the current exploitation rates, very few snapper live to be more than 10 years of age, so that there is very little information about cohort size for any of the cohorts produced during the 1970s.

The environmental model with process error indicated high variation in recruitment for the whole time period (Fig. 1B). This is due to the formulation of the recruitment submodel, for which the annual anomalies are anomalies from the temperature-recruitment relationship; if there is no information in the data about recruitment for a particular year, the recruitment will follow the temperature-recruitment relationship.

The correlation of the estimated recruitment from the traditional model with SST had a low *r*-square (0.26), but it was statistically significant at the 0.05 level when a two-tailed test was used. In addition, the slope of the relationship between recruitment and SST was much less for the traditional model than for to the environmental model with process error (Table 3). The estimates of recruitment from the traditional model included a large number of estimates that were close to the mean because there was no information in the data about these recruitments. Therefore, it was inappropriate to use these recruitments to correlate with SST and, if used, they would result in a poor fit. However, a significant correlation, as obtained in this application, suggests that the correlation is probably stronger than apparent from the analysis, which should give confidence that a relationship exists and provide an incentive to apply the integrated models.

The environmental model with process error did not show a statistically significant improvement over the environmental model because, ignoring the 1970s data, the catch-at-age data were available only for the last part of the time period. The recruitment anomalies were estimated for the whole time period, as well as for the initial conditions. Many of these recruitment anomalies had very little information associated with them and therefore did not add anything to the estimation procedure. However, they do add additional parameters, which reduce the possibility of accepting the model when using the likelihood ratio test. If the recruitment anomalies were estimated for only a limited number of years, it is likely that the environmental model with process error would be a statistically significant improvement over the environmental model. Statistical tests could be carried out to determine which annual recruitment anomalies should be estimated, but this would be very time consuming. Reducing the number of annual recruitment anomalies may also cause an underestimation of the confidence intervals. For the snapper example, removing the anomalies for the initial conditions may be a good compromise.

Discussion

We have developed a general framework for integrating environmental time series into stock assessment models that appears to perform better than traditional methods. The method is flexible and it can be used to model many different functional relationships between population or fishing processes and environmental time series and to include multiple environmental time series for any population model parameter (see Appendix II). Furthermore, it can be used with any statistical stock assessment model. The method can be used to test whether an environmental time series describes temporal variation in model parameters.

The traditional model, which estimates annual recruitment within the stock assessment model and subsequently correlates the recruitment with the environmental series outside the stock assessment model, performs poorly. It has a reasonable probability of detecting a relationship between recruitment and the environmental series, but this probability decreases rapidly as the number of years with missing catch-at-age data sets increases. The probability of incorrectly detecting a relationship when one is not present is low. This method has reasonable confidence-interval coverage for average recruitment and little bias or variance in the estimates of model parameters. The factor causing the poor performance of the traditional model is the large bias in the estimate of the slope of the relationship between recruitment and the environmental time series, which increases as the number of years with missing catch-at-age data increases. The bias occurs because the traditional model has a penalty on the absolute size of the annual recruitment deviations. This penalty constrains an annual recruitment anomaly to be close to the mean recruitment when there is little or no information about the recruitment in that year. Therefore, when the logarithm of the annual recruitment is correlated with the environmental time series, the estimated slope of the relationship is biased downward. Even in situations for which there is sufficient information for every recruitment anomaly, there will be a small tradeoff in the size of the anomaly, which reduces the contribution of the penalty to the objective function and the likelihood from the catch-at-age data. Unfortunately, if the penalty on the annual recruitment anomalies is removed, the estimation process can become unstable, particularly in data-poor situations for which the bias is greater. The amount of time that is required by the estimation algorithm also increases if the penalty is removed. When the penalty on the size of the recruitment anomalies is removed, the bias in estimates of the slope of the relationship between recruitment and the environmental time series is reduced when using all the catch-at-age data, but the variance in the estimates is greatly increased. In addition, when removing the penalty there was a large positive bias when using only the last 10 years of catch-at-age data and a large negative bias when using only the first 10 years of catch-at-age data. It is not known what results would be obtained if cohort analysis, which does not use a constraint on the annual recruitment anomalies, is used instead of the statistical catch-at-age analysis. It should be remembered that cohort analysis cannot be used or assumptions that are unlikely to be satisfied will have to be made when catch-at-age data are missing for some years.

The environmental model, which has a deterministic relationship between recruitment and the environmental time series that is integrated into the stock assessment model, also performs poorly. This method has poor confidence interval coverage for average recruitment because the size of the confidence intervals are greatly underestimated. The method has larger bias and variance in the estimates of model parameters compared to the other two methods. There is a small negative bias in the estimate of the slope of the relationship between recruitment and the environmental time series. The environmental model has a very high probability of detecting a relationship between recruitment and the environmental series, and this probability only decreases slightly as the number of missing years of catch-at-age data sets increases. However, this model has a very large probability of incorrectly detecting a relationship when one is not present. Therefore, when using the environmental model, the likelihood ratio test should not be used to determine if there is a significant relationship between recruitment and an environmental time series. The value used to compare to the χ^2 statistic in the likelihood ratio test for the environmental model is highly correlated with the catch-at-age sample size; therefore simulation analysis is needed to find the appropriate χ^2 statistic for the given sample size (see Appendix III). This is also important for calculating confidence intervals that are also based on the χ^2 statistic and is the reason for the poor coverage for R_0.

The environmental model with process error, which has a relationship between recruitment and the environmental time series that is integrated into the stock assessment model with additional process error, performs well. This model has a reasonable probability of detecting a relationship between recruitment and the environmental series, but this probability is lower than those of the other two models, and decreases as the amount of data is reduced. It has a low probability of incorrectly detecting a relationship when one is not present. These probabilities could be improved by using simulation analysis to find the appropriate χ^2 statistic (see Appendix III). This method has reasonable confidence interval coverage for average recruitment and has little bias or variance in the estimates of model parameters. There is very little bias in the estimate of the slope of the relationship between recruitment and the environmental time series.

For the environmental model with process error, when there is little or no information in the data to estimate the recruitment for that year, the penalty on the annual recruitment anomalies causes recruitment to be estimated close to the recruitment predicted by the relationship between recruitment and the environmental time series. Therefore, if there is a relationship between recruitment and the environmental time series, this model should provide better estimates because additional information is included in the estimation procedure. This model has the favorable property that if there is no relationship between recruitment and the environmental time series, the model estimates β to be small, eliminating any influence of the relationship between recruitment and the environmental time series, and still estimates the annual recruitment anomalies to represent the variation in annual recruitment. The likelihood ratio test can be used to detect a relationship between recruitment and the environmental time series, and if a relationship does not exist, the results with β fixed at zero can be used. However, including β in the estimation procedure, even when there was no relationship between recruitment and the environmental time series, did not increase the error in the parameter estimates in relation to the model with β fixed at zero (see the results for the traditional model, Table 1D).

The method we describe can be used to integrate environmental time series for parameters of the stock assessment model other than recruitment. The influence of the environment on catchability of the fish would be an obvious choice because there are numerous publications on the topic. For example, Green (1967) suggested that thermocline data would improve estimation of tuna abundance from catch and effort data, by allowing for the differentiation between changes in tuna abundance and catchability due to vertical distribution of tunas influenced by temperature. We have used a method similar to the method that is presented in the present study to incorporate SST into the purse-seine catchability parameters for yellowfin and bigeye tuna (Maunder and Watters, 2001; Watters and Maunder, 2001). Maunder (2001a) presented a general method to integrate the standardization of CPUE data into stock assessment models, including the integration of environmental variables. Growth rates have been observed to have temporal variation, and this variation has been correlated with environmental factors. Several authors have presented growth curves that include temperature data (e.g. Mallet et al., 1999). Movement is another process that may be influenced by the environment. Lehodey et al. (1997) showed that spatial shifts in the western Pacific skipjack tuna population are linked to the movement of a large pool of warm water and that the movements of this large pool are related to El Niño-Southern Oscillation events.

Once a correlation between the environmental time series and the population process has been determined, this relationship can be used to improve the predictive ability of the model. For example, if a relationship between SST at the time of spawning and recruitment has been determined, and the age at recruitment to the fishery is 3 years, recruitment to the fishery can be estimated 3 years in advance. One should be cautious about assuming that these relationships are valid and will continue to hold into the future, however. Hilborn and Walters (1992) cautioned about using environmental data because there are many environmental indices that one can try, and if the data set has a few large and a few small observations, it is likely that one of the environmental data sets will correlate with the data. Myers (1998) reviewed a number of published correlations between recruitment and environmental factors and found that few of the correlations held when retested at later dates. Maunder and Starr (1998) also advised caution because they found that a strong cohort may not enter the fishery when expected because of variations in growth rates. We have found that, when applying this method to the bigeye tuna data, there is an inconsistency in the pre-1997 data and the data for 1997 and 1998 caused by much stronger than expected year classes entering the fishery in 1997 and 1998. There is also difficulty in deciding on the management strategy if environmental regime shifts are influencing the productivity of the stock (Maunder, 1998b). An advantage of the integrated approach, particularly the environmental model with process error, is that it more fully describes the uncertainty in the relationship between the population process and the environmental time series, and therefore this uncertainty can be included in any management advice based on the relationship.

Conclusions

Integrating environmental relationships in a statistical stock assessment model is an improvement over the traditional statistical model when there are large gaps in the data. However, it is important to include process error to avoid the high probability of detecting spurious correlations seen in the environmental model when using the likelihood ratio test. Therefore, the environmental model with process error is the model of choice because 1) there is no bias in the estimates, 2) when there is no relationship with the environmental series, it is equivalent to the traditional model, 3) when such a relationship exists, the recruitment estimates are improved, particularly if there are important gaps in the data, 4) it may be used for prediction, and 5) uncertainty about the relationship can be modeled.

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Appendix I: description of simulator and estimator

The following is a description of the model equations used for the data simulator and for the estimator. The model is run from an unexploited state at the start of the fishery for 20 years. The model includes 10 age classes, where the 10th age class is a plus group.

Dynamics

$$N_{y,1} = R_0 \exp(\beta I_y + \varepsilon_y^R + \alpha) \tag{I.1}$$

$$\alpha = \ln\left(\frac{n}{\sum \exp(\varepsilon_y^R + \beta I_y)}\right) \tag{I.2}$$

$$N_{y,a} = \left(N_{y-1,a-1}(1-u_{y-1}s_{a-1})\right)e^{-M_{a-1}} \text{ for } a < A \tag{I.3}$$

$$\begin{aligned} N_{y,A} &= \left(N_{y-1,A-1}(1-u_{y-1}s_{A-1})\right)e^{-M_{A-1}} \\ &+\left(N_{y-1,A}(1-u_{y-1}s_A)\right)e^{-M_A} \end{aligned} \tag{I.4}$$

$$u_y = \frac{C_y}{B_y} \tag{I.5}$$

$$B_y = \sum_a N_{y,a} s_a w_a \tag{I.6}$$

where Ny,a = the numbers in age class a at the beginning of year y;
R_0 = the average recruitment;
ε_y^R = the recruitment anomaly for year y;
σ_R^2 = the standard deviations for the recruitment anomalies;
M_a = the age specific natural mortality rate;
A = the maximum age used in the analysis;
u_y = the exploitation rate in year y;
s_a = the selectivity to the fishing gear for age a individuals;
C_y = the total catch in weight for year y;
B_y = the exploitable biomass for year y; and
w_a = the weight for an individual of age a.

Initial conditions

$$N_{1,a} = R_0 e^{\left(-\sum_{i=1}^{a-1} M_i\right)} \text{ for } 1 < a < A \tag{I.7}$$

$$N_{1,A} = \frac{N_{1,A-1}e^{(-M_{A-1})}}{1-e^{-M_A}} \tag{I.8}$$

Simulation

$$\varepsilon_y \sim N(0, \sigma^2_R) \tag{I.9}$$

$$I_a \sim N(0, \sigma^2_I) \tag{I.10}$$

$$\varepsilon_a^{CPUE} \sim N(0, \sigma^2_{CPUE}) \tag{I.11}$$

$$CPUE_y = qB_y \exp(\varepsilon_y^{CPUE} - 0.5\,\sigma^2_{CPUE}) \tag{I.12}$$

where q = the catchability coefficient for the CPUE index;
σ_I = the standard deviation for the variation in the recruitment index;
ε_a^{CPUE} = the observation error in the CPUE index; and
σ_{CPUE} = the standard deviation of the error in the CPUE index.

$$D_{y,a} \sim Multinomial\left(\frac{C_{y,a}^{numbers}}{\sum_a C_{y,a}^{numbers}}, n = 50\right) \tag{I.13}$$

$$C_{y,a}^{numbers} = N_a u_y s_a, \tag{I.14}$$

where $D_{y,a}$ = the number of individuals of age a in the catch-at-age same in year y; and
n = the number in the catch-at-age sample; and
σ_{CPUE} = the catch in numbers of age a individuals in year y.

Estimation

The likelihood values can be calculated by using the following equations:

$$-\ln L(\theta \mid I) = \sum_y \left[\ln(\sigma_{CPUE}) + \frac{\left(\ln(CPUE_y) - \ln(qB_y)\right)^2}{2\sigma^2_{CPUE}}\right] \tag{I.15}$$

$$-\ln L(\theta \mid D) = -\sum_{y,a} D_{y,a} \ln(p_{y,a}) \tag{I.16}$$

$$p_{y,a} = \frac{C_{y,a}^{numbers}}{\sum_a C_{y,a}^{numbers}} \tag{I.17}$$

The penalities (priors) on the annual recruitment anomalies can be calculated by using the following equation:

$$-\ln \text{ Prior } (\varepsilon^R) = \sum_y \left[\frac{(\varepsilon_y^R)^2}{2\sigma_R^2}\right]. \tag{I.18}$$

The following values were used for the biological parameters:

$$w_a = l_a^3, \tag{I.19}$$

$$l_a = 1 - e^{-0.1}, \tag{I.20}$$

and $M = 0.2$ and $s = 1$, where the a for M and s are subscripted.

Appendix II: extensions

The recruitment-environmental submodel that we used to analyze the snapper stock is simple, and other submodels may improve the fit to the data and the explanatory ability of the environmental time series. A dome-shaped relationship has been observed between abundance of tuna larvae and SST (Forsbergh, 1989), indicating that a quadratic or higher-order polynomial submodel may be more appropriate.

$$R_t = \exp(\alpha + \beta_1 I_t + \beta_2 I_t^2 + \ldots \beta_n I_t^n + \varepsilon_t). \tag{II.1}$$

Regime-switching models (Granger, 1993) that have the ability to favor two levels of values may be more appropriate for species that are hypothesized to experience two environmental regimes.

$$X_t = \left\{ (ub - lb)\left[1 + \exp\left(-\ln(19)\frac{I_t - I_{50}}{I_{95} - I_{50}} \right) \right]^{-1} + lb \right\} \exp(\varepsilon_t), \tag{II.2}$$

where lb = the lower bound of the model parameter (low regime);
ub = the upper bound of the model parameter (high regime);
I_{50} = the environmental time series value that gives a 50% influence; and
I_{95} = the environmental time series value that gives a 95% influence.

If I_{95} is only slightly higher than I_{50}, the model will have two regimes. Therefore, the model can be simplified by setting I_{95} as a small fixed value above I_{50}, allowing for the use of a regime-shifting model that requires estimation of only the lower bound, upper bound, and the value of the environmental time series at the point of change.

The method can be easily extended to include multiple environmental factors,

$$X_t = \mu \exp\left(\varepsilon_t + \sum_i \beta_i I_{i,t} + \alpha \right), \tag{II.3}$$

where i indexes the environmental factor.

The method we have used assumes that recruitment is independent of spawner biomass (i.e. we penalize the deviation from a mean recruitment modified by the relationship with the environmental time series). Maunder (1998a) suggested applying the method to stock-recruitment relationships, and the models described by Hilborn and Walters (1992, p. 285–287) could be used to integrate spawner-recruitment models and environmental time series into the stock assessment model.

$$R_t = f(S_t)\exp(\beta I_t + \varepsilon_t + \alpha), \tag{II.4}$$

where $f(S_t)$ = the function for the stock-recruitment relationship and
S_t = the spawning biomass at time t.

The equation for the Ricker (1954) and Beverton and Holt (1957) models would be

$$R_t = S_t \exp(a - bS_t)\exp(\beta I_t + \varepsilon_t + \alpha). \quad \text{Ricker} \tag{II.5}$$

$$R_t = \frac{aS_t}{b + S_t}\exp(\beta I_t + \varepsilon_t + \alpha), \quad \text{Beverton-Holt} \tag{II.6}$$

where a and b are parameters of the stock recruitment models.

Appendix III: the hypothesis test problem for the environmental model

Let, $\hat{p}_j = \dfrac{n_j}{N}$

where $N = \sum_j n_j$

is the sample size and n_j is the number from category j in the sample. The negative log-likelihood (ignoring constant) is

$$-\ln L = N \sum_j -\hat{p}_j \ln(p_j).$$

$$\chi^2 = 2(\ln L_1 - \ln L_0) = 2N\left(\sum_j \hat{p}_j \ln(p_{1,j}) - \sum_j \hat{p}_j \ln(p_{0,j}) \right),$$

therefore χ^2 is proportional to N. LnL_1 (estimate β) has one more parameter than LnL_0 (β=0) and therefore will be at least slightly larger (two sets if independent random numbers always have a nonzero correlation). Therefore, there will be some value of N for which χ^2>3.84. Now, consider a simple example where

$$p_j = \frac{x_j}{\sum_j x_j} \text{ and } x_j = \mu \exp(\beta I_j + \varepsilon_j),$$

$$\text{with the penalty } -\ln \text{ Prior } (\varepsilon \mid \sigma) = \sum_j \frac{(\varepsilon_j)^2}{2\sigma^2},$$

and σ is a constant. Consider two models: 1) $\varepsilon_j = 0$ and 2) estimate ε_j. For model 1, as N increases χ^2 increases in proportion to N, as explained above, because the penalty term is constant. However, for model 2, as N gets large, the relative size of the penalty compared to $-\ln L_0$ gets smaller and therefore the estimates of ε_j change so that p_i gets closer to $\hat{p}_i$. Therefore, for model 2, χ^2 does not increase proportionally with N.

An appropriate test for the environmental model would be to produce sets of random environmental indices that have the same variance and auto-correlation as the actual environmental index to determine the appropriate value of χ^2 that would give the desired type-I error. This test would overcome the sample size effect. The method could also be used to refine the test for the environmental model with process error.

Abstract—We examined the spatial and temporal distribution, abundance, and growth of young-of-the-year (YOY) Atlantic croaker (*Micropogonias undulatus*) in Delaware Bay, one of the northernmost estuaries in which they consistently occur along the east coast of the United States. Sampling in Delaware Bay and in tidal creeks in salt marshes adjacent to the bay with otter trawls, plankton nets and weirs, between April and November 1996–99, collected approximately 85,000 YOY. Ingress of each year class into the bay and tidal creeks consistently occurred in the fall, and the first few YOY appeared in August. Larvae as small as 2–3 mm TL were collected in September and October 1996. Epibenthic individuals <25 mm TL were present each fall and again during spring of each year, but not in 1996 when low water temperatures in January and February apparently caused widespread mortality, resulting in their absence the following spring and summer. In 1998 and 1999, a second size class of smaller YOY entered the bay and tidal creeks in June. When YOY survived the winter, there was no evidence of growth until after April. Then the YOY grew rapidly through the summer in all habitats (0.8–1.4 mm/d from May through August). In the bay, they were most abundant from June to August over mud sediments in oligohaline waters. They were present in both subtidal and intertidal creeks in the marshes where they were most abundant from April to June in the mesohaline portion of the lower bay. The larger YOY began egressing out of the marshes in late summer, and the entire year class left the tidal creeks at lengths of 100–200 mm TL by October or November when the next year class was ingressing. These patterns of seasonal distribution and abundance in Delaware Bay and the adjacent marshes are similar to those observed in more southern estuaries along the east coast; however, growth is faster—in keeping with that in other northern estuaries.

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Seasonal distribution, abundance, and growth of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) in Delaware Bay and adjacent marshes*

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Atlantic croaker (*Micropogonias undulatus*) is a commercial and sport fishery species that inhabits demersal habitats in estuarine, coastal, and continental shelf systems along the Atlantic coast of North America and in the Gulf of Mexico (Joseph, 1972). They spawn primarily over the continental shelf during a protracted spawning season that, based on the presence of larvae along the Atlantic coast, may extend from early July through March (Lewis and Judy, 1983; Cowan and Birdsong, 1985; Warlen and Burke, 1990; Hettler et al., 1997; Nixon and Jones, 1997; Able and Fahay, 1998). The exact location of spawning in the Middle Atlantic Bight (MAB) may be related to the areal extent of favorable warm bottom waters for spawning (Norcross and Austin, 1988) and may sometimes occur within or close to the mouth of Chesapeake Bay (Barbieri et al., 1994b; Reiss and McConaugha, 1999). The larvae and postlarvae have been observed to be more abundant in deeper layers of water that may facilitate transport into and retention within estuarine nursery areas (Weinstein et al., 1980; Norcross, 1991). The young-of-the-year (YOY) usually begin to enter estuaries and tidal creeks along the Atlantic coast in September, or occasionally August, and they are often common components of the fish fauna in tidal creeks and estuaries until fall of the next year from New Jersey southward along the Atlantic coast and in the Gulf of Mexico (Chao and Musick, 1977; Knudsen and Herke, 1978; Weinstein, 1979; Currin et al., 1984; Ross, 1988; Able and Fahay, 1998). In some years there is a second pulse of small YOY that arrives in estuaries along the Atlantic coast in the spring or summer; this pulse may be the offspring from later spawning (Chao and Musick, 1977; Ross, 1988). In general, the YOY use estuarine habitats with salinities ranging from almost pure freshwater to seawater (Miglarese et al., 1982).

Although YOY Atlantic croaker are present in some Atlantic coast estuarine habitats during the winter (Haven, 1957; Bearden, 1964; Dahlberg, 1972; Chao and Musick, 1977; Shenker and Dean, 1979; Bozeman and Dean, 1980; Able and Fahay, 1998), they appear to experience winter mortality in the MAB in years with unusually cold winters (Massman and Pacheco, 1960; Joseph, 1972; Chao and Musick, 1977; Wojcik, 1978). Recent laboratory studies have found that YOY Atlantic croaker do not survive in sustained water temperatures of 3°C or lower (Lankford and Targett, 2001); therefore extended periods of low winter water temperatures may have drastic effects on their overwinter survival in some estuaries.

Previous studies have indicated that YOY Atlantic croaker reach about 107–187 mm TL after their first year of growth in estuaries along the Atlantic coast and 102–250 mm TL in the Gulf of Mexico (Knudsen and Herke, 1978), but only a few studies have reported seasonal growth rates (Hansen, 1969; Knudsen and Herke, 1978). Length-frequency based growth rate estimates for the first year of growth for YOY along the Atlantic coast have ranged from 0.32 to 0.41 mm/d (Knudsen and Herke, 1978). However, these were based on the entire year, including the larval and early juvenile period when analysis of otolith daily growth rings indicates much slower growth rates of 0.18–0.41 mm/d during the fall and winter months (Nixon and Jones, 1997). Length-frequency data from estuarine nursery areas clearly indicate that most growth occurs during the spring and summer months (Haven, 1957; Chao and Musick, 1977; Ross, 1988; Able and Fahay, 1998).

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Despite various studies of YOY Atlantic croaker in some areas of the Atlantic and Gulf coasts, there is relatively little known of their early life history near the northern part of their range in the MAB and this is especially true for Delaware Bay. Our four-year study used extensive collections in Delaware Bay and in adjacent tidal marsh creeks to describe the timing of Atlantic croaker ingress, their seasonal abundance and size, growth rates, and the timing of their egress out of the marshes.

Methods

Study sites

Delaware Bay is the estuary of the Delaware River and encompasses about 1878 km^2 of open water along the southern edge of New Jersey and the northern edge of Delaware (Fig. 1). It has a relatively deep area (10–30 m) in the middle of the lower bay, bordered by narrow shoals and flanked by extensive tidal flats and salt marshes, which contain an additional 85.5 km^2 of open water in tidal creeks bordered by approximately 640 km^2 of marsh-plain area. Depending on the amount of river discharge, salinities range from 30–31‰ at the mouth of the bay, to 1–10‰ in the lower Delaware River (Table 1; Cronin et al., 1962; Garvine et al., 1992).

Ichthyoplankton survey

Catch data from an ichthyoplankton survey (Table 2) was used to analyze the distribution, abundance, and size of larval Atlantic croaker in Delaware Bay and the lower Delaware River from April to October 1996. Sampling was performed during daylight hours once a month in April and October and twice a month from May to September. Each sampling period included one tow at 70 randomly selected stations distributed among eight designated sampling zones (Fig. 1). Samples were collected with a 1-m diameter plankton net (0.5-mm mesh) deployed with a depressor in single stepwise oblique tows from the surface to the bottom. Tows were made at a speed of 1.4–1.9 knots for four to six minutes in the direction of the tidal flow. Up to 50 individuals were measured to the nearest millimeter total length (TL) from each sample.

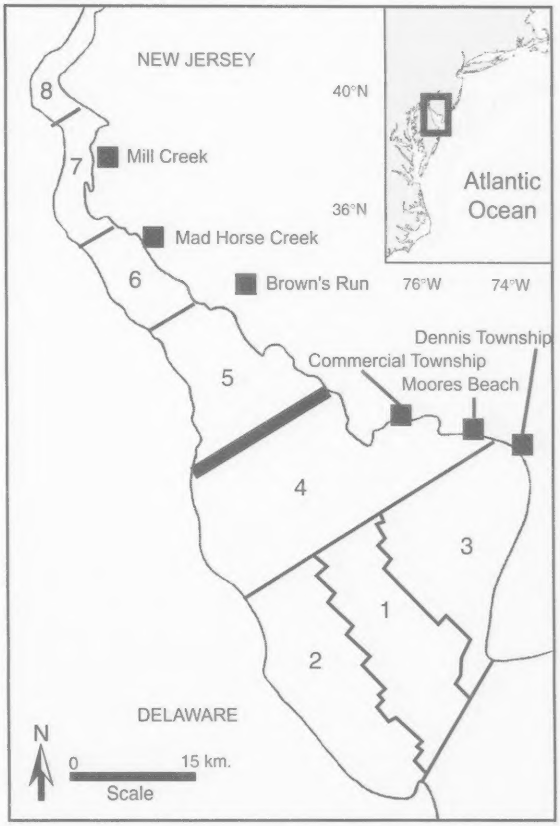

Figure 1

Locations of salt marsh tidal creek sampling sites (1996–99) and designated sampling zones (1–8) in the Delaware Bay and in the lower Delaware River for the ichthyoplankton (April–October 1996) survey and the otter trawl (April–October 1996–98) survey. The heavier line across the bay indicates the boundary between the upper (5–8) and lower (1–4) sampling zones and marsh sites.

Otter trawl survey

We used catch data from a three-year otter trawl survey (Table 2) to analyze the distribution, abundance, and growth of settled YOY Atlantic croaker in Delaware Bay and the lower Delaware River. Sampling was performed during daylight hours twice a month from April to October in 1996 and once a month in 1997 and 1998, at 40 stations divided up among the same eight sampling zones of the ichthyoplankton survey (Fig. 1). Station locations were selected by using a stratified random sampling design from a grid of 1002 stations, excluding the stations over the deepest water near the mouth of the bay in zone 1. There were eight stations sampled each month in zone 3, six in zone 4, and four in all the other zones. Trawling was done with 4.9-m otter trawls (6 mm stretched codend mesh), made against the prevailing direction of the tide at a speed of 1.8 m/sec for 10 minutes. Up to 100 individuals were measured from each sample. For presentation

Table 1

Physical characteristics of marsh and adjacent bay study sites located along the New Jersey shore of Delaware Bay, 1996–99. See Figure 1 for locations of individual sites.

Marsh site	Surface temp. range (°C)	Average surface temp. (°C)	Surface salinity range (‰)	Average surface salinity (‰)	Average surface dissolved oxygen (mg/L)
Upper bay					
Mill Creek	5.0–29.0	19.5	0–8.4	2.8	7.4
Mad Horse Creek	0–31.0	19.2	0.7–23.0	9.1	6.3
Browns Run	7.0–31.3	20.5	0.2–14.0	7.0	5.4
Bay	7.0–28.0	20.2	1.5–17.8	10.2	6.3
Lower bay					
Commercial Township	8.0–30.0	19.8	4.5–22.9	17.0	6.8
Upper Moores Beach	2.0–30.0	18.7	10.0–23.8	17.2	6.2
Lower Moores Beach	5.0–29.0	19.0	4.0–25.0	18.9	7.0
Dennis Township	6.0–32.0	20.4	6.2–24.7	17.0	5.7
Bay	6.0–29.1	19.6	11.1–24.7	17.8	7.3

Table 2

Yearly catch per unit of effort (CPUE=number of fish per tow or weir set) for the different types of gear in the marsh creeks or in Delaware Bay and the total number of Atlantic croaker collected by each type of gear. RUMFS = Rutgers University Marine Field Station; EEP = Public Service Enterprise Group Estuary Enhancement Program.

	1996 CPUE	1997 CPUE	1998 CPUE	1999 CPUE	Total number of tows/sets	Total number of fish	Source
Marsh creeks							
Otter trawl (creeks)	2.4	3.8	19.1	3.9	4,654	36,295	RUMFS
Otter trawl (bay)	164.6	15.3	29.3	49.5	336	12,755	RUMFS
Weir	1.1	41.6	46.8	98.7	443	20,714	RUMFS
Delaware Bay							
Otter trawl	4.6	2.8	19.7	—	1,438	13,497	EEP
1-m plankton net	1.7	—	—	—	957	1,638	EEP
Total fish	8,671	12,350	43,942	19,936	7,828	84,899	

and statistical analysis of some aspects of the data of the ichthyoplankton and otter trawl surveys in the bay, the upper four zones were combined into an upper bay region and the lower four combined into a lower bay region (Fig. 1).

Marsh creek survey

Tidal creek sampling was carried out at six salt marsh sites on the New Jersey side of Delaware Bay (Fig. 1, Table 1). Dennis Township, Commercial Township, and Moores Beach will be referred to collectively as the lower bay sites, and Browns Run, Mill Creek, and Mad Horse Creek will be referred to as the upper bay sites. The average depth of the trawling stations (1.3–2.6 m) and Secchi depth values (0.3–0.4 m) were similar at all sites. The upper bay sites in the mostly oligohaline region of the bay had average salinities of 2.8–9.1‰ and the lower bay sites were in the mesohaline region with average salinities of 17.0–18.9‰ (Table 1).

We sampled each of the marshes (Fig. 1) monthly from April through November 1996–99 (Table 2). Small intertidal marsh creeks were sampled with weirs set at high tide and hauled at low tide, approximately six hours later. Each weir (2.0 m × 1.5 m × 1.5 m, with 5.0 m × 1.5 m wings, 6.0-mm stretched mesh) consisted of a funnel-shaped net stretched across the channel with wings extended back onto the marsh surface from each end of the net. In cases when the creek did not drain completely the area in front of the weir was seined into the weir.

Trawling in larger intertidal to subtidal marsh creeks took place around high tide and consisted of four replicate two-minute tows per station, made against the current with a 4.9-m otter trawl (6-mm stretched codend mesh) towed at a constant engine RPM of 2500. Trawling station locations at each site were designed to sample fishes along the mouth to upper creek gradients (see Able et al., 2000; 2001; Able et al.[1]). Thus, at each of the marshes there were six trawling locations. These locations included two large subtidal creeks and two smaller creeks with lower subtidal and upper subtidal or intertidal sections in each of the latter. Additional trawling locations were established in the bay immediately outside the mouth of the large creek at the Dennis Township, Moores Beach, Commercial Township, and Mad Horse Creek study sites (Fig. 1). The fish collected at these bay stations were used in the length-frequency figures for the bay (exclusive of November when there was no trawl survey sampling in the bay) and for the growth calculations, but not in the catch-per-unit-of-effort (CPUE) calculations for the bay. Atlantic croaker collected in each weir set and in each trawl were enumerated, and up to 50 individuals per weir set and 20 per trawl were measured to the nearest millimeter total length. Abundances (CPUE, number of fish per trawl) were compared between the upper and lower bay sites in Delaware Bay, among the six different marsh sites, and among years, by using the nonparametric Mann-Whitney *U*-test, or the Kruskal-Wallis ANOVA of ranks for multiple comparisons, and when differences were found, the Dunnís test was used (criteria for significance: $P<0.05$) to make pair-wise comparisons.

Physical variables were measured at the end of each weir and otter trawl sample in the marshes and in Delaware Bay (Table 1). Temperature, salinity, and dissolved oxygen concentrations were measured with a hand-held salinity, temperature, and oxygen meter (YSI Model 85), by lowering the probe into the water and recording surface values. Water transparency was measured by lowering a Secchi disc into the water column until it was no longer visible and recording the corresponding depth in 0.1-m increments.

Growth

Growth rates for YOY Atlantic croaker were calculated for samples collected during the late spring through fall in the upper and lower regions of the bay in 1997 and 1998 and in the upper and lower bay marsh sites during 1997, 1998, and 1999. We compared growth using the progression of the monthly median lengths in each area by computing the change in the median length of a cohort over a time period divided by the number of days in the period. This method was based on the following assumptions: 1) no new (small) recruits join the population during the calculation interval, and 2) no (large) individuals leave the population over the calculation interval. To best meet these assumptions, median growth rates were calculated by using the monthly length data from May to July when there was a minimum of movement of fish between different areas, and then for longer-term monthly comparisons, from May to August, September, and October when fish were moving out of the marshes into the bay. The smaller-size cohort present in the bay in June and July 1998 and in the marshes in 1999 was excluded from the growth calculations for those years. The linearity of the progression of median lengths was tested by using linear regression, and the resulting lines were compared between the upper and lower bay.

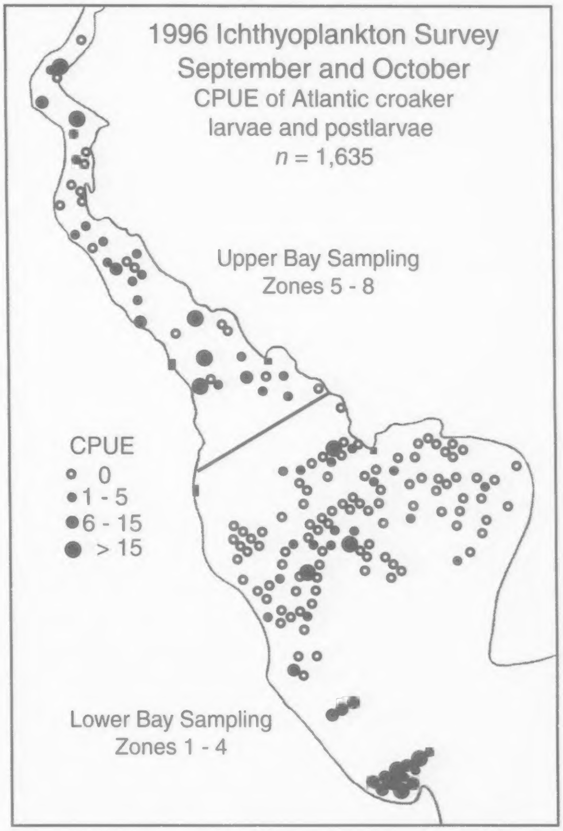

Figure 2

Catch per unit of effort (CPUE) of larval and postlarval Atlantic croaker (*Micropogonias undulatus*) collected in the ichthyoplankton survey in September and October 1996.

Results

Distribution, abundance, and size during fall ingress and settlement

Atlantic croaker larvae were collected only in the late summer and fall during the ichthyoplankton survey in Delaware Bay in 1996 (Figs. 2 and 3). A few individuals were first collected in August (n=3, CPUE=0.02 fish/tow), and then large numbers of larvae were collected through September (n=639, CPUE=3.6) and October (n=996, CPUE=9.0), but they were absent from April to July. The overall September–October CPUE was 9.0 fish/tow (range:

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[1] Able, K. W., D . M. Nemerson, and T. M. Grothues. In review. Evaluating salt marsh restoration in Delaware Bay: continued analysis of fish response at former salt hay farms.

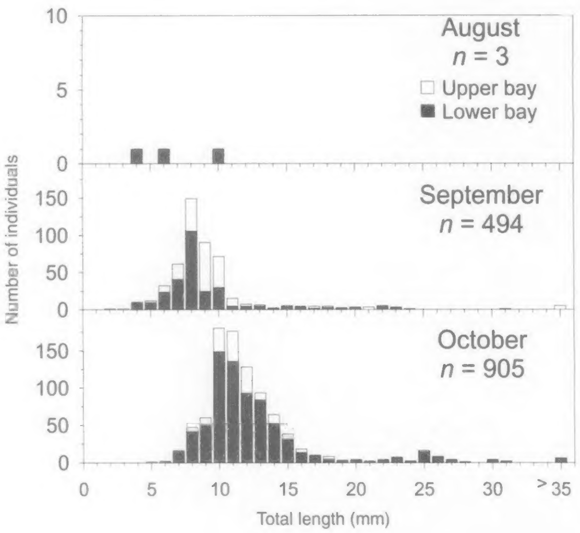

Figure 3

Length-frequency distributions of larval and postlarval Atlantic croaker (*Micropogonias undulatus*) collected in the upper and lower regions of Delaware Bay during the ichthyoplankton survey in 1996.

0–56) in the upper bay zones 5–8 and 4.9 (range: 0–36) in the lower bay zones 1–4 (Figs. 1 and 2), and these CPUE values were significantly different between zones ($P=0.03$). At least one individual was collected in each of the eight zones in both September and October; the highest two-month combined CPUE occurred in the uppermost zone 8 (CPUE=13.4), followed by zone 5 (CPUE=9.6), and the lowest occurred in zone 3 (CPUE=0.1). Larvae were 4–10 mm during August (all in zone 2), predominantly 2–24 mm in September, and 5–28 mm in October (Fig. 3)—the smallest individuals being caught in the lower bay.

Benthic YOY Atlantic croaker of a variety of sizes first appeared in substantial numbers in September in the otter trawl surveys in both the bay (Fig. 4) and marshes (Fig. 5) at lengths >5 mm, and with modes of 15–30 mm for the primary cohort. Exceptions occurred in the bay in 1997, when they were not collected by the trawl survey until October and when they were not collected during September at two of the three upper bay marsh sites each year.

The CPUE of benthic YOY Atlantic croaker was usually highest during October in the lower bay marshes (Fig. 6). This pattern of abundance is illustrated by the much higher four-year overall CPUE of recently ingressed YOY, especially at Dennis Township, Commercial Township, and Upper Moores Beach (Fig. 7). The combined four-year CPUE values were significantly different ($P<0.001$) at each of the six sites, and the CPUE values at the Dennis Township site were significantly greater than at all the sites except for Commercial Township. Similarly, Commercial Township was different from all sites except Dennis Township and Upper Moores Beach, and Upper Moores Beach also was different from Browns Run in the upper bay.

Recently settled YOY Atlantic croaker were also caught in the weirs in small intertidal marsh creeks during September, October, and November in all three years; the majority were collected at the Dennis Township marsh in the lower bay (Fig. 8). The monthly CPUE (fish per set) in the weirs at Dennis Township was greatest in October 1997 and November 1999 (the weirs were not in place until October 1996) and the largest total number was collected during 1999. The combined four-year CPUE values for 1996–99 at each of the six sites were significantly different ($P<0.001$), and the CPUE values at the Dennis Township site were significantly greater than those at all the sites, except Commercial Township.

The monthly CPUE values during ingress in the bay also were highest in October, but in contrast to the marsh sites were usually higher in the upper part of the bay (Fig. 6). The combined CPUE values for September and October were significantly different between the upper and lower bay regions in 1998 ($P<0.001$) and 1997 ($P=0.048$), but not in 1996 ($P=0.51$). The combined CPUE values for September and October for each year (1996–98) were significantly different among years ($P<0.001$) and were different between 1996 and 1997, and between 1996 and 1998.

A second, smaller cohort of YOY Atlantic croaker appeared in the bay in June and July 1998 and in the tidal

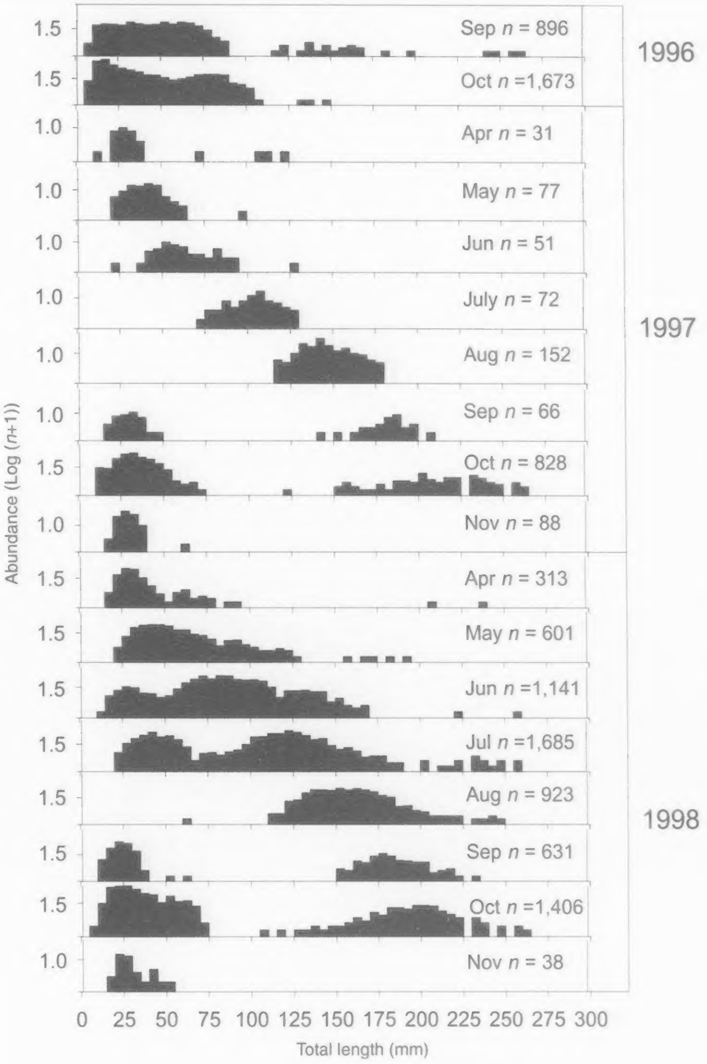

Figure 4

Length-frequency distributions of log (n+1) transformed numbers of Atlantic croaker (*Micropogonias undulatus*) collected by otter trawl between April and November in Delaware Bay from 1996 to 1998. None were collected in the bay from April to August of 1996.

creeks in June 1999 (Fig 4). In the bay these were as small as 15 mm in June 1998 and had a mode of 26–30 mm. They were even more abundant in the bay during July 1998 and had a mode of 41–45 mm. Individuals of this cohort were collected at five of the eight zones in the bay during June and July but were rare in subsequent months (Fig. 4). A smaller size cohort of YOY (n=69 fish) also appeared in the marshes (Fig. 5) and in the associated bay stations in June 1999.

Distribution, abundance, and habitat use during summer residency

Young-of-the-year Atlantic croaker were abundant in Delaware Bay and in the adjacent marsh creeks from April through the fall egress of each year, except in 1996, when trawling in both the marshes and the bay caught no YOY until 26 individuals (115–200 mm) were collected in the bay in September and October (Fig. 4). In contrast, the

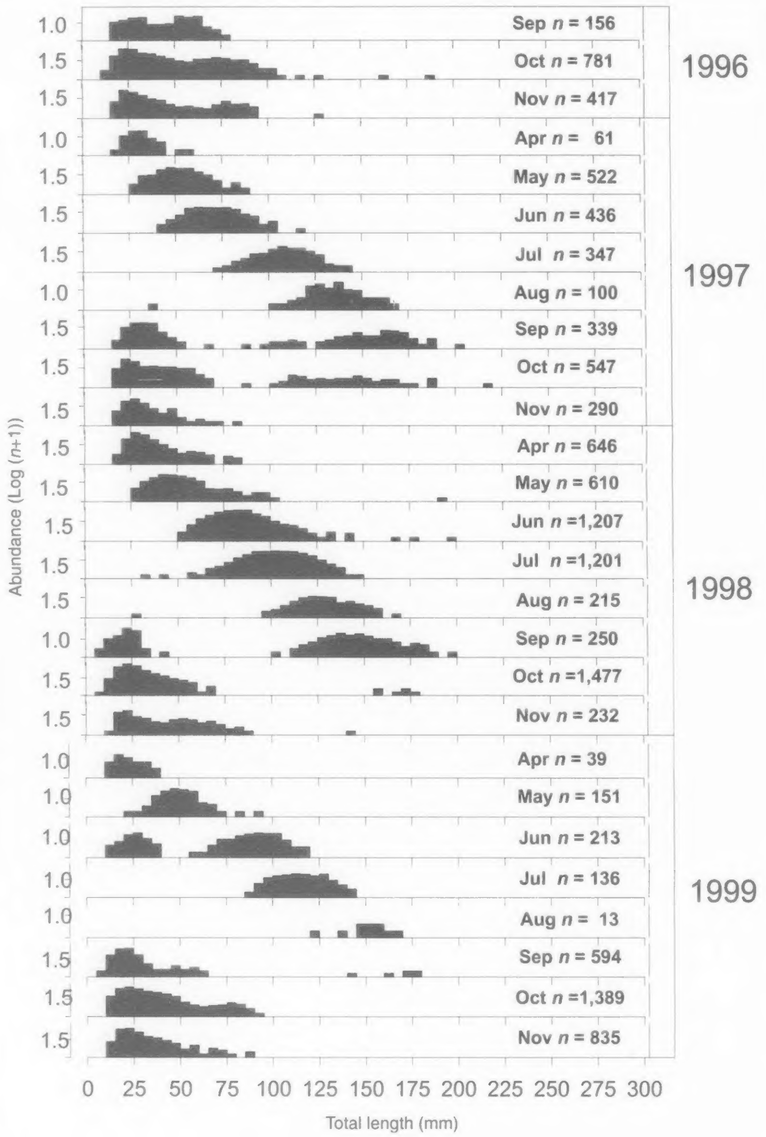

Figure 5

Length-frequency distributions of log (n+1) transformed numbers of Atlantic croaker (*Micropogonias undulatus*) collected by otter trawl (April to November) in salt marsh creeks along the northern shore of Delaware Bay from 1996 to 1999. None were collected in the marshes from April to August of 1996.

marsh creek surveys found YOY in both the large and small creeks from April to September during 1997, 1998, and 1999. Typically in the years after 1996, the CPUE was greatest from April to June at the lower bay marsh sites and then decreased after July to an almost total absence of fish toward the end of the fall egress out of the marshes in November (Fig. 6). The overall CPUE at each marsh site for all three year classes combined (April to November in 1997, 1998 and 1999) was highest at Dennis Township and Commercial Township and at Upper Moores Beach in the lower bay and lowest at Lower Moores Beach and at the upper bay sites (Fig. 7). As a result, the monthly

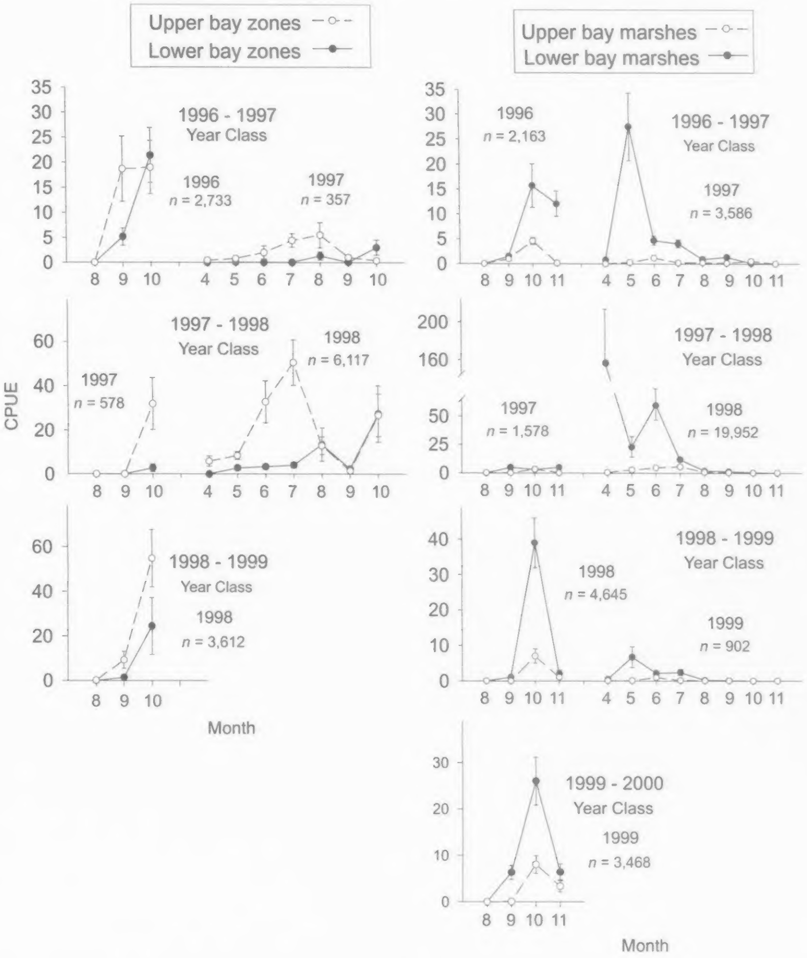

Figure 6

Monthly average catch per unit of effort (CPUE ±SEM) of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) collected by otter trawl during the fall ingress and from April to November for three year classes in the upper and lower regions of Delaware Bay (left panels: CPUE=fish/10 min. tow) and of four year classes in tidal creeks at the upper and lower bay marsh sites (right panels: CPUE=fish/2 min. tow). No data are presented from April to July of 1996 because Atlantic croaker were absent from the bay and marshes until October.

CPUE at the lower bay marshes was consistently more than twice as high as that in the upper bay (Fig. 6). The combined four-year CPUE values for YOY caught during April–October 1997–99, at each of the six sites were significantly different ($P<0.001$), and the CPUE values at the Dennis Township site were significantly greater than at each of the other sites. The CPUE values at Commercial Township and Upper Moores Beach in the lower bay also were greater than those at all the upper bay sites.

Young-of-the-year Atlantic croaker also used small intertidal creeks in the marshes from April to August, where they were collected in weirs. They were most abundant at the Dennis Township site in the lower bay in all three years where they were present from May to July in 1997 and from April to August in 1998, 1999 (Fig. 8). The monthly CPUE (fish per set) in the weirs at Dennis Township was greatest in June of both 1997 and 1998. Compared to the total catch in the weirs at Dennis Township in all three years (n=3994), far fewer were caught in the weirs at the other sites in the lower bay during all three years (n=152) and fewer still at the sites in the upper bay (n=9). The CPUE of YOY Atlantic croaker in Delaware

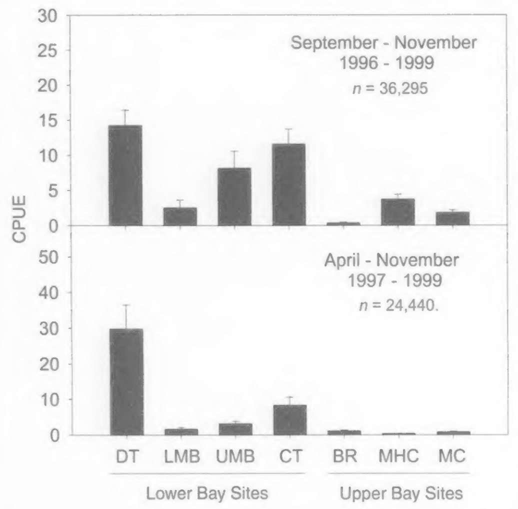

Figure 7

Combined overall average catch per unit of effort (CPUE= fish/2 min. tow [±SEM]) of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) collected by otter trawl at the Dennis Township (DT), Lower Moores Beach (LMB), Upper Moores Beach (UMB), Commercial Township (CT), Browns Run (BR), Mad Horse Creek (MHC) and Mill Creek (MC) marsh sites during the fall ingress of four years (1996–99) and of post-ingress croaker (April to November 1997–99).

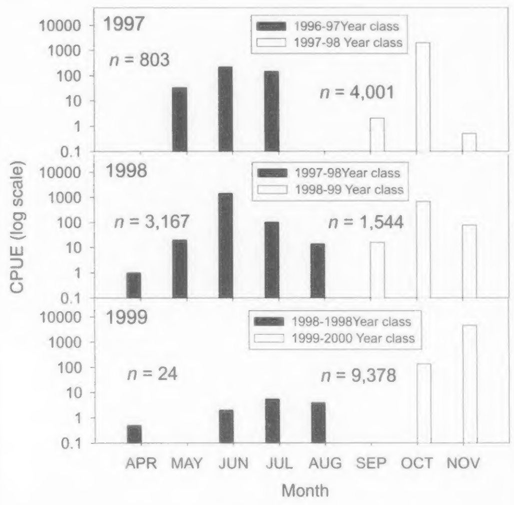

Figure 8

Catch per unit of effort (CPUE, fish/set) of four year classes of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) caught each year in the two monthly weir sets across small intertidal creeks at the Dennis Township marsh site in the lower bay during the fall ingress (white bars) and during spring and summer of the following year (black bars).

Bay was higher in the upper bay, which has mud sediments in most areas, and was much higher in 1998 than in 1997. The monthly CPUE in the upper bay peaked in July or August, but in the lower bay it peaked in October of both years (Fig. 6). The combined CPUE values in the upper and lower bay zones were different between the two regions in both 1997 and 1998 ($P<0.001$) and the catches within each region were different between the two years ($P<0.001$).

During the summer most YOY were collected in areas of Delaware Bay that had muddy sediments (Fig. 9). In the upper bay zones 7 and 8, which likely have mostly pure mud sediments, YOY were collected at 82% of the stations. In contrast, they were absent in the deeper, large central area of the lower bay that has predominantly sandy and gravelly sediments. However, in the shallow portion of the lower bay, sandy mud, muddy sand, and gravelly mud sediments appear to be distributed on both sides of the bay, and YOY were almost exclusively collected over or near these substrates from April to August.

Growth

Although YOY Atlantic croaker showed rapid growth during the summer, there was no evidence of growth during the winter. The median growth rates for YOY Atlantic croaker calculated for two- to five-month periods beginning in May were fast and ranged from 0.5 to 1.5 mm/d (Table 3). They were slightly higher in the bay than in the marshes (avg.=1.2 mm/d in the bay and 0.9 mm/d in the marshes) and were lowest in 1998 when Atlantic croaker were most abundant. The growth rates dropped off in the marshes when calculated from May to September or October (Table 3). The lowest early summer growth rates occurred in the tidal creeks in the lower bay in 1998 when the CPUE was the highest. The growth rates in the upper and lower regions of Delaware Bay were similar in each year, but as in the lower bay marshes, the values were lower in 1998 when YOY were much more abundant. Linear regressions of the median lengths used to calculate these growth rates showed that median length was strongly correlated to date (P=0.02–0.001) and illustrated the slightly slower growth rates at the lower bay sites in both 1997 and 1998 (Fig. 10). These pairs of regression lines were not significantly different (ANCOVA) for upper and lower bay regions of either the marsh sites in 1997 (P=0.1), or in the bay in 1998 (P=0.6), except in 1998, when a lower growth rate was indicated at the lower bay marsh sites (P=0.03). In 1999, a similar linear progression of median lengths was observed in the lower bay marshes (r^2=0.98), but sample sizes were too small in the upper bay for growth-rate calculations. Although there was no sampling in the winter, the length-frequency distributions indicated that most fish collected in April in the bay and marshes were the same

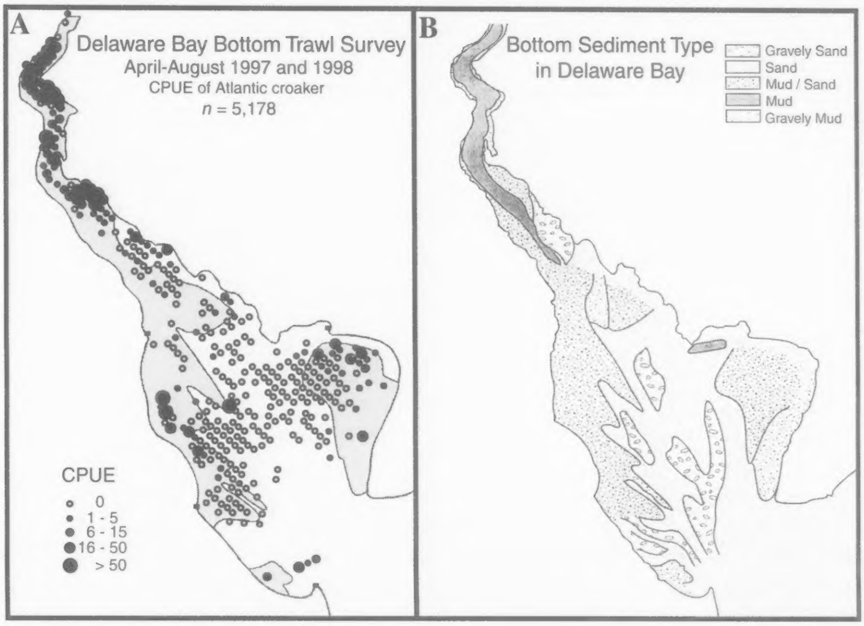

Figure 9

(**A**) Catch per unit of effort (CPUE=fish/10 min. tow) of young-of-the-year Atlantic croaker *(Micropogonias undulatus)* collected by otter trawl (April to August in 1997 and 1998). Sediments containing mud are indicated by shading. (**B**) The distribution of specific bottom sediment types in Delaware Bay is modified from Sharp (personal commun. [J. H. Sharp. Marine Studies, Univ. Delaware, Lewes, DE.]).

size or smaller than the ingressed fish collected during the previous fall of all three years (Figs. 4 and 5).

Consistent with the above fast growth rates, YOY Atlantic croaker reached lengths of about 70–140 mm by July and lengths ranging from 90 to 170 mm by August in the marshes and slightly larger in the bay (Figs. 4 and 5). As a result of these fast growth rates, the YOY attained a size of approximately 125–250 mm by September, approximately 12 months after ingress into the bay and adjacent marshes, and were distinctly larger than the next year class that began ingressing during September of each year.

Egress

Young-of-the-year Atlantic croaker showed a relatively consistent pattern of egress out of the marsh creeks in the late summer and fall of each year, and as a result, there was an increase in CPUE in the bay during October of both years. The monthly CPUE in both upper and lower bay marshes declined during the summer and were low by August in all three years (Fig. 6), but the number of fish present appeared to drop off more rapidly from August to October in 1999 than in other years (Figs. 5 and 6). In the bay, CPUE began to decrease somewhat later, after July or August, but then increased to the yearly maximum for the lower bay in October 1997 and 1998. By November of each year, almost all YOY appeared to move out of the marshes at sizes <200 mm, but in the bay there were large individuals >250 mm caught in October 1997 and 1998. The baywide trawling survey did not provide samples in November, so it was impossible to determine the timing of egress of the remaining YOY out of the bay, but very few age-1 fish were present in the bay or marshes by spring of the next year.

Discussion

Ingress and settlement

Young-of-the-year Atlantic croaker ingress into bay and marsh nursery areas starting in the fall of each year in Delaware Bay and in other estuaries along the Atlantic coast. The majority appeared in September, October, and November during our study and in previous collections in Delaware Bay (Able and Fahay, 1998), Chesapeake Bay (Haven, 1957; Chao and Musick, 1977), and North Carolina (Ross, 1988). However, the fall ingress of this cohort was not evident until October in Georgia (Dahlberg, 1972) and December in South Carolina (Bearden, 1964). The sudden appearance of significant numbers of larger fish (50–75 mm) in September 1996 in both the bay and marshes and to some extent in the marshes in 1999 suggests that individuals that experienced different growth rates or came from different spawning events sometimes occurred simultaneously in Delaware Bay.

Table 3

Estimated daily growth rates of young-of-the-year Atlantic croaker *(Micropogonias undulatus)* based on the monthly progression of median lengths in the upper and lower regions of Delaware Bay in 1997 and 1998 (see Fig. 1) and in tidal creeks in the marsh sites adjacent to the upper and lower bay in 1997, 1998, and 1999. Growth rate calculations were made for periods of two to five months, with each period starting in May. Calculations for locations with sample sizes <10 fish were excluded.

Habitat	Year	Location in bay	Average collection date	Sample size	Median length (mm TL)	Median growth rate (mm/d)
Delaware Bay	1997	Upper bay	17 May	25	33	—
			7 July	71	103	1.37
			5 Aug	88	143	1.38
			2 Sep	16	183	1.39
			2 Oct	10	190	1.14
		Lower bay	26 May	52	43	—
			16 Aug	64	154	1.35
			20 Sep	14	187	1.23
			4 Oct	96	218	1.34
	1998	Upper Bay	13 May	275	41	—
			15 Jul	873	121	1.27
			10 Aug	433	144	1.16
			6 Sep	45	177	1.17
		Lower Bay	15 May	326	57	—
			19 Jul	220	140	1.28
			16 Aug	490	164	1.15
			10 Sep	131	182	1.06
Marsh Creeks	1997	Upper Bay	21 May	17	46	—
			17 Jul	13	115	1.21
			20 Aug	16	154	1.19
			14 Oct	33	120	0.51
		Lower Bay	26 May	505	52	—
			23 Jul	334	110	1.00
			26 Aug	84	132	0.87
			21 Sep	99	161	0.92
			19 Oct	13	150	0.67
	1998	Upper Bay	8 May	142	41	—
			8 Jul	348	115	1.21
			5 Aug	41	143	1.15
			2 Sep	23	153	0.96
		Lower Bay	13 May	467	50	—
			14 Jul	851	100	0.81
			11 Aug	174	125	0.83
			9 Sep	126	142	0.77
	1999	Lower Bay	18 May	148	49	—
			18 Jul	128	114	1.07
			15 Aug	12	151	1.15

According to the sizes of individuals captured by plankton net in the water column, versus those collected by otter trawl on the bottom, settlement may occur over a broad size range, i.e. approximately 10–40 mm TL. Scale formation in Atlantic croaker begins at 14–16 mm SL and is completed at 31–38 mm SL during this time (Bridges, 1971) and is an indicator of transformation between larval and juvenile stages. Alternatively, collection of overlapping sizes in water column and bottom samples may imply frequent vertical movements as could occur during tidal stream transport (see Weinstein et al., 1980, for recent examples). These movements would provide an appropriate mechanism for small YOY to reach the bay and the lower Delaware River as has been suggested for larval Atlantic croaker in Chesapeake Bay (Norcross, 1991).

The length-frequency data from our study and from previous studies along the Atlantic coast indicate that a second, less-abundant cohort of YOY Atlantic croaker often enter nursery areas during the spring and summer. This second cohort (between 10 and 45 mm) was observed in June 1998 and 1999 during our study and in May or August (20–30 mm) in the York River of the Chesapeake Bay (Chao and Musick, 1977). Similarly, a second mode was usually apparent from April through August during three years in North Carolina creeks and bays (Ross, 1988), and in May in Georgia (Dahlberg, 1972). In South Carolina, a second smaller cohort began appearing in March and subsequently became the dominant mode in June and July (Bearden, 1964). In addition, the larger-size individuals that have appeared during the fall months simultaneously with the ingressing fall cohort during our study and in the Chesapeake Bay (Haven, 1957; Chao and Musick, 1977), may be individuals of this late-arriving second cohort that did not enter the Chesapeake and Delaware bays until fall.

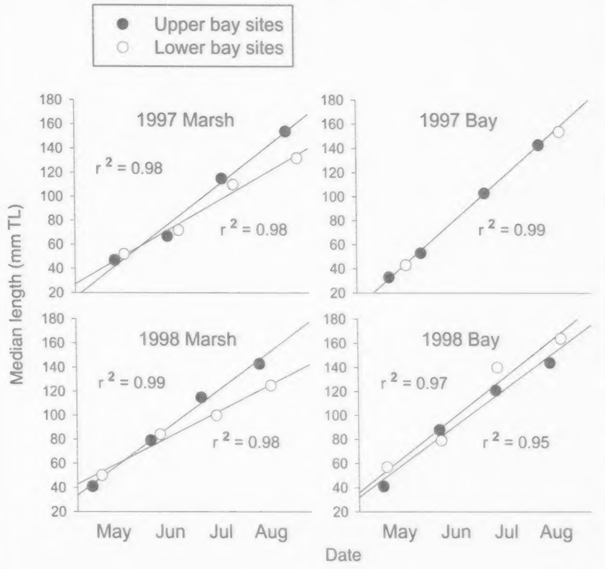

Figure 10

Linear regressions and goodness-of-fit measures of the monthly median total lengths of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) caught at the upper bay (open circles) and lower bay (black circles) marsh sites and regions of Delaware Bay from May to August in 1997 and 1998 (see Table 3). The coefficient of determination is shown in the upper left for the upper bay regression lines and in the lower right for the lower bay. There is no regression for the lower bay because sample sizes in this region during June and July of 1997 were too small.

These late arrivals to nursery areas in the Chesapeake and Delaware bays may be individuals that were spawned close to or south of Cape Hatteras in late winter because there is no evidence of spawning in late winter or spring north of Cape Hatteras in the MAB. Atlantic croaker larvae were caught only from August to January 1977–1987 over the continental shelf in the MAB and while entering estuaries in central New Jersey (Able and Fahay, 1998), or from November to February in coastal Virginia (Cowan and Birdsong, 1985). In contrast, just south of Cape Hatteras, larvae as small as 5.2 mm SL were present in collections made from October through mid-April within and offshore of the Newport River estuary in North Carolina in both 1972–73 and 1973–74 (Lewis and Judy, 1983). Small larvae also were collected in the same estuary from November through mid-April in 1985–1986 (Warlen and Burke, 1990) and 1991–92 (Hettler et al., 1997) and in the Cape Fear estuary from mid-March to Mid-April in 1978 (Weinstein et al., 1980). Together, these studies indicate that late winter spawning occurs and suggests that it takes place south of Cape Hatteras. Analysis of otolith microstructure of larval and juvenile Atlantic croaker from the MAB indicates that later spawned larvae and juveniles have slower growth rates (Warlen, 1982; Nixon and Jones, 1997), which may account for the much smaller size of the later-arriving cohort when it enters the Chesapeake and Delaware bays during the late spring and early summer.

Ross (1988) suggested that there may be two groups of Atlantic croaker that overlap and mix in North Carolina. The first group, occurring from North Carolina southward through the northern Gulf of Mexico, with a tendency toward high mortality, lower longevity, early maturation, results from winter spawning (White and Chittenden, 1977; Barger, 1985) and mostly spring recruitment to estuaries. The second group ranges from North Carolina to about New Jersey and may exhibit lower mortality, higher longevity, greater size at age, late summer–fall spawning, mostly fall recruitment, and greater size at maturity (Wallace, 1940; Morse, 1980; Barbieri et al., 1994a). However, the group of larger, older Atlantic croaker observed by Ross (1988) apparently has been absent in Chesapeake Bay in recent years (Barbieri et al., 1994b). Lankford et al. (1999) did not find statistically significant genetic differences between fall-spawned YOY Atlantic croaker from north of Cape Hatteras and spring-spawned YOY from south of Cape Hatteras, but YOY from the Gulf of Mexico were genetically discrete from those from the Atlantic coast. This lack of marked genetic differences north and south of Cape Hatteras is not surprising if there is southward migration of adults from the MAB during winter as has been suggested (Haven, 1957). Although, spawning and recruitment to nursery areas does appear to occur later in the South Atlantic Bight (Bearden, 1964) and in the Gulf of Mexico (Pearson, 1929; Suttkus, 1955; Hansen, 1969), more research is needed to determine if there are significant biological differences between adults in these two areas and if the late arriving YOY in the north originate from spawning at or south of Cape Hatteras.

Habitat use

Young-of-the-year Atlantic croaker in this study used the entire range of marsh creek habitats, i.e. small intertidal creeks and large subtidal creeks within the study area. Intensive tag and recapture studies in marsh creeks at the Dennis Township site found that YOY were resident for periods of up to 78 days from July through October 1998 (Miller and Able, 2002). As a result, our interpretations of habitat use and growth may be representative for much of the summer and fall in Delaware Bay marsh creeks.

In the deeper water of the bay, YOY were collected throughout the whole range of salinities but were most abundant over the predominantly pure mud sediments in the lower Delaware River and over areas with mud sediments elsewhere in the lower bay. This pattern is evident elsewhere because YOY have been reported to be most abundant over soft mud sediments in Apalachicola Bay in the Gulf of Mexico (Kobylinski and Sheridan, 1979). As in Delaware Bay, YOY have been collected over the full range of salinities in South Carolina (Bearden, 1964; Miglarese et al., 1982) and Georgia (Dahlberg, 1972). However, laboratory experiments suggest that lower salinities are metabolically less costly for YOY (Moser and Gerry, 1989; Peterson et al., 1999) and that in some areas of Chesapeake Bay, YOY are most abundant in regions with low salinities (<18‰) (Haven, 1957).

Habitat use and survival in the winter may vary between estuaries. Young-of-the-year Atlantic croaker appear to overwinter in estuaries in the Gulf of Mexico (Pearson, 1929; Suttkus, 1955; Hansen, 1969; Knudsen and Herke, 1978) and in the South Atlantic Bight (Bearden, 1964; Dahlberg, 1972; Bozeman and Dean, 1980), but in the MAB there is probably significant overwinter mortality in years with particularly cold winters. The YOY appear to overwinter in some estuarine habitats in the York River region of Chesapeake Bay in most years (Haven, 1957; Chao and Musick, 1977) and in deeper areas of the bay (Welsh and Breder, 1923), but in some years YOY have been observed to experience winter mortality based on their subsequent disappearance after a cold period (Massman and Pacheco, 1960) and on direct observations of mass mortalities and collections of dead YOY in years with unusually cold winters (Joseph, 1972; Chao and Musick, 1977, Wojcik, 1978). Further, analysis of long-term recruitment indices for Atlantic croaker from 1979 to 1993 indicates that the YOY of this species may have experienced winter mortality due to low water temperatures in 30% of the years in Chesapeake Bay and 74% of the years in Delaware Bay (Lankford and Targett, 2001).

Overwintering mortality apparently occurred in Delaware Bay in 1996 when water temperatures in the region dropped below 3°C and remained below 4°C for an extended period of time. The NOAA Buoy 4409, located in the ocean just south of the mouth of Delaware Bay, recorded water temperatures at about 2–4°C for 18 days during January and February 1996, which is at or below the approximate survival temperature of 3°C determined in laboratory experiments (Lankford and Targett, 2001). This apparently resulted in a total absence of YOY throughout the bay and in marsh creeks during the spring and summer, which is not surprising because temperatures in the estuary were likely cooler than in the ocean. In contrast, during the winters preceding the relatively high catch years of 1997 and 1998, water temperatures at the same location never dropped below 4.4°C during the winter of 1996–97 or below 5.6°C during 1997–98.

Growth

Growth rates that we calculated in both upper and lower regions of the Delaware Bay (two years) and in the marshes (three years) ranged from about 0.8 to 1.4 mm/d from May to July. The strong linear correlation between median length and date suggested that the average growth rates were relatively constant during the summer from May to August before egress from marshes. Seasonal growth rates of YOY Atlantic croaker in other estuaries along the Atlantic coast may be similar to those in Delaware Bay, but the way in which they were calculated influences the values. Knudsen and Herke (1978) reviewed the apparent growth rates of YOY Atlantic croaker from a variety of sources but presented growth rates only for the entire first year of growth, which were all less than 0.5 mm/d for studies along the Atlantic coast and in the Gulf of Mexico. However, these estimates included both larval and overwintering periods; therefore they probably underestimated the growth rates during the summer when growth rates are highest. Monthly modal progression in published lengths indicate relatively fast growth rates during the summer in estuarine areas south of Delaware Bay. Our calculation of modal progression in lengths from May to July in various parts of the York and Pamunkey rivers of Chesapeake Bay suggested growth rates of approximately 1.3 and 0.7 mm/d in 1952 and 1953, respectively (Haven, 1957) and of 0.9 mm/d in 1972 (Chao and Musick, 1977). Similarly, calculated values for May to July for fish from shallow creeks in North Carolina indicated growth rates of 0.6, 0.8, and 0.9 mm/d in 1979, 1980, and 1981, but the 1979 estimate is likely to be an underestimate because many of the larger fish appeared to be moving into deeper habitats during that time period (Ross, 1988). In our study, the growth rates remained relatively high when calculated through October (1.1–1.3 mm/d) in the bay but dropped off in the marshes (0.5–0.7 mm/d), potentially reflecting the egress of larger YOY out of the marshes into the bay.

Data from the Gulf of Mexico suggest slower growth rates of YOY Atlantic croaker in some areas but egress of larger fish out of the sampling area may also bias these estimates. Hansen (1969) used length-frequency data to determine growth rate estimates of 0.3 mm/d from January through August in the Pensacola Estuary on the Florida gulf coast in both 1964 and 1965 but noted the highest growth rates were in July (0.6 mm/d). Knudsen and Herke (1978) estimated growth of YOY in a semi-impounded marsh in Louisiana using recaptured individuals sprayed with fluorescent pigment during winter and spring and found rates of 0.4–0.5 mm/d for fish marked in late January and early February and recaptured into March. Rates for those marked mid-February to late March and recaptured into May were 0.8–0.92 mm/d. A previous study at the same location, using the same techniques, estimated that fish marked from December to March and recaptured into June grew at about 0.47 mm/d (Arnoldi et al., 1974). The monthly length-frequency data from Lake Pontchartrain, Louisiana (Suttkus, 1955), indicated a constant but slow growth rate of 0.3 mm/d from February to September 1954, and no increase in growth rate during the summer. As a result of the above, it appears that growth rates may be faster, and thus countergradient in more northern populations, as suggested for *Menidia* (Conover and Present, 1990), but care should be taken in interpreting growth rates from the literature, especially those based on modal progression.

Egress

Young-of-the-year Atlantic croaker have a regular pattern of egress out of tidal creeks and estuaries in the MAB during the late summer and fall after reaching lengths of about 100–250 mm. As we observed in the Delaware Bay system, the majority left the marsh creeks from August to October at lengths <200 mm. The larger individuals appeared to leave the marshes first, as has been observed elsewhere (Haven, 1957; Yakupzack et al., 1977), and almost all had left by November. However, the CPUE increased in Delaware Bay in October of both years, and this may have been caused by fish egressing out of the marshes into the bay. Large individuals remained in Delaware Bay longer than in the marshes and substantial numbers of fish 150–300 mm were present in the bay in September and October. This finding suggests that egress from the tidal creeks caused the disappearance of Atlantic croaker there, and not gear avoidance, because large fish continued to be caught in the bay. The exact timing of egress of the majority of Atlantic croaker out of the bay is unclear due to lack of sampling throughout the bay after October. However, previous collections in Delaware Bay have shown no evidence of any individual >100 mm from November to March (Able and Fahay, 1998), suggesting that egress out of the bay is finished by November in some years. The same pattern of egress out of nursery habitats in the fall has been observed in Chesapeake Bay (Haven, 1957), but in some years there were substantial numbers of fish present into November (Chao and Musick, 1977). Very few of each year class reappear in collections during the spring and summer of the next year in either Chesapeake or Delaware bays (Haven, 1957; Chao and Musick, 1977; Able and Fahay, 1998) and therefore the fate of these individuals is unknown.

Fall egress also occurs out of estuaries in the South Atlantic Bight and the Gulf of Mexico, but in contrast to the Chesapeake and Delaware bays, more Atlantic croaker appear to either remain through the winter or re-enter these habitats in some areas in late winter or early spring. In North Carolina, egress out of tidal creeks was mostly completed by November, but this same year class was present again as age-1 fish in the bays in March, April, and May when sampling resumed (Ross, 1988). A similar pattern of egress from estuaries was observed in South Carolina, but the reappearance of age-1 fish in February was even more prominent and they continued to be collected until fall (Bearden, 1964). In the Gulf of Mexico, some age-1 fish have been observed to remain in estuarine habitats for an additional year in Lake Pontchartrain, Louisiana (Suttkus, 1955), or reappear from January to April after leaving the study area in December in coastal Texas (Pearson, 1929).

In summary, this study presents the first comprehensive examination of YOY Atlantic croaker seasonality and habitat use in Delaware Bay and the adjacent marshes. Although patterns of habitat use and seasonality are similar along the east coast, some divergence from the seasonal patterns in Delaware Bay are evident in estuaries in the South Atlantic Bight and the Gulf of Mexico. Growth estimates appear to be the most divergent of any characteristics examined—faster growth rates occurring in the more northern estuaries such as Delaware Bay.

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Age validation, growth, mortality, and additional population parameters of the goldband snapper (*Pristipomoides multidens*) off the Kimberley coast of northwestern Australia

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Abstract—Goldband snapper (*Pristipomoides multidens*) collected from commercial trap and line fishermen off the Kimberley coast of northwestern Australia were aged by examination of sectioned otoliths (sagittae). A total of 3833 *P. multidens*, 80–701 mm fork length (98–805 mm total length), were examined from commercial catches from 1995 to 1999. The oldest fish was estimated to be age 30+ years. Validation of age estimates was achieved with marginal increment analysis. The opaque and translucent zones were each formed once per year and are considered valid annual growth increments (the translucent zone was formed once per year between January and May). A strong link between water temperature and translucent zone formation was evident in *P. multidens*. The von Bertalanffy growth function was used to describe growth from length-at-age data derived from sectioned otoliths. No significant differences in length-at-age were found between sexes and growth parameters were L_∞ = 598 mm, K = 0.187/yr, t_0 = –0.173 (r^2=0.76). Regression models of estimated age as a function of otolith and fish measurements indicated a significant relationship between estimated age and otolith weight (r^2=0.94). Total instantaneous mortality (Z) estimates generated from catch-at-age data of *P. multidens* from the northern demersal scalefish fishery (NDSF) were 0.65 for 1995–96, 0.87 for 1996–97, and 0.71 for 1997–98. Estimates of the annual instantaneous rate of natural mortality (M) were 0.10–0.14. The NDSF population of *P. multidens* is considered to be exploited above optimum levels on the basis of these mortality estimates. The protracted longevity, moderately slow growth and low natural mortality rates of *P. multidens* predisposes this species as one vulnerable to overfishing, thus cautious management strategies will be required. Furthermore, capture of *P. multidens* from depths of 60 meters or greater results in a high mortality of fish because the physoclistous ruptures causing internal hemorrhaging and hence there is a low probability of survival of any fish returned to the sea. Thus traditional harvest strategies involving size limits will be inappropriate for these fish. Conversely, harvest strategies that include appropriately targeted spatial fishery closures may provide a useful additional means of preserving the spawning stock biomass of these fish and protect against recruitment overfishing.

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The goldband snapper (*Pristipomoides multidens*, Day), known also as goldbanded jobfish, Day's jobfish and large-scaled jobfish, is widely distributed throughout the tropical Indo-Pacific Ocean region from Samoa in the Central Pacific to the Red Sea in the Western Indian Ocean and from southern Japan south to Australia (Allen, 1985). Along Western Australia, *P. multidens* is found as far south as Cape Pasley (34°S) and is landed in commercial quantities from the Ningaloo Reef area (23°30'S) northwards (Kailola et al., 1993; Newman, unpubl. data). They inhabit hard bottom areas and areas of vertical relief and large epibenthos from depths of 60 to at least 245 m and are concentrated in depths from 80 to 150 m (Allen, 1985; Newman and Williams, 1996).

Pristipomoides multidens is a commercially important species throughout much of its range, forming an important part of the landed catch in both artisanal and developed fisheries (Dalzell and Preston, 1992; Newman, 2001). In Western Australia this highly valued resource is marketed whole, usually fresh on ice, and transported by road from regional ports to markets in most state capital cities. It is occasionally exported. In the Kimberley region, within the northern demersal scalefish fishery (NDSF), *P. multidens* has composed on average 37.7% of the landed catch from 1995 to 1999 (contributing on average 255 metric tons (t)/year). In terms of value to fishermen, it is second only to the red emperor snapper (*Lutjanus sebae*).

Information on the biology of *P. multidens* is limited. The juvenile habitats of *P. multidens* have not been identified, although Newman (unpubl. data) obtained juveniles from uniform sedimentary habitat with no relief. In previous studies, several age determination techniques were used to determine the age of *P. multidens* but there were limited attempts at age validation (Edwards, 1985; Mohsin and Ambak, 1996; Richards[1]). The accurate determination of fish age is the key to estimating growth rates and mortality. Errors in determining fish age can result in ambiguous demographic parameters and provide misleading impressions of the production potential of fish stocks (Newman et al., 2000a). There is a lack of reliable information on the longevity, growth parameters, mortality rates, and population characteristics of *P. multidens*, despite its ecological and commercial importance.

This work represents the first comprehensive study of age, growth, and mortality of a population of *P. multidens* based on age estimates from sectioned otoliths and contributes to the management of these stocks. The objectives of this study were to validate aging and to provide age, growth, mortality and population characteristics of *P. multidens* from the Kimberley region of Western Australia that are based on age estimates from sectioned otoliths.

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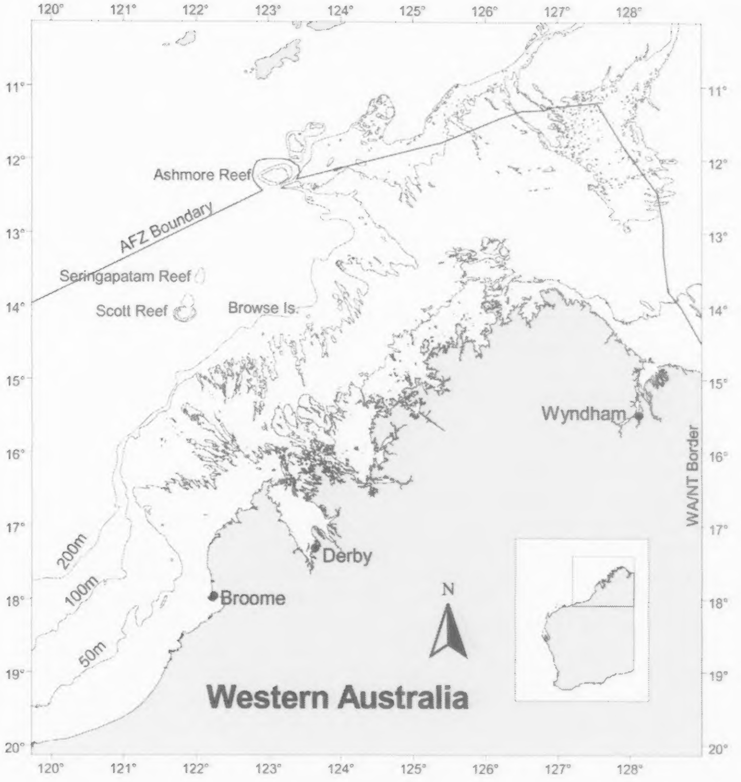

Figure 1

Location of the northern demersal scalefish fishery (NDSF) off the Kimberley coast of northwestern Australia showing the 50-m, 100-m, and 200-m depth contours. The NDSF is bounded in the west by the 120°E latitude line, to the north by the boundary of the Australian fishing zone (AFZ), and to the east by the border with the Northern Territory. Fishing primarily occurs in depths of 80–140 m.

A further objective was to investigate the relationship between estimated age and the measurements of both otolith and fish dimensions to assess the applicability of these measurements in predicting the age of this species.

Materials and methods

Commercial landings of *P. multidens* from the NDSF off the Kimberley coast of Western Australia were sampled from 1995 to 1999. Samples were acquired opportunistically from July 1995 to December 1996, whereas samples obtained from January 1997 to December 1999 were collected on a monthly basis among all vessels in the fleet. All specimens were captured with fish traps at depths of 60 to 200 m from 12°–20°S latitude (Fig. 1). Additional specimens were attained from research vessel cruises with fish traps.

All fish were measured to the nearest mm total length (TL), fork length (FL) and standard length (SL), weighed to the nearest g total weight (TW) and cleaned weight (CW), and where possible, sex was determined by examination of the gonads. Cleaned weight is defined as the TW after removal of the gills and viscera. Length measurements were used to derive conversion equations with linear regression models [$TL=a + b\ (FL)$, $FL=a + b\ (TL)$, $FL=a + b\ (SL)$ and $SL=a + b\ (FL)$].

Length-weight models

The relationships between FL and both TW and CW were described by the power function

$$W = aL^b,$$

where W = weight (TW or CW, g); and
L = FL (mm).

These relationships were fitted to log-transformed data and the parameters were back-transformed (with correction for bias) to the above form.

Analysis of covariance (α=0.05) was used to determine if there were significant differences in the weights-at-length (FL) relationships between sexes for *P. multidens*. Length and weight data were transformed to natural logarithms to satisfy assumptions of normality and homogeneity. Multiple comparisons were performed with Tukey's honestly significant difference (HSD) test. Trends in mean length and weight of fish over time were assessed by using analysis of variance (α=0.05).

Otolith preparation and analysis

Otolith removal, measurement, and preparation followed the procedures and protocols described in Newman et al. (1996), Newman et al. (2000b), and Newman and Dunk (2002). All age estimates were based on the analysis of thin transverse sections of otoliths. These thin sections were examined under a dissecting microscope at 10–30× magnification with reflected light on a black background.

The otoliths from eight juvenile *P. multidens* (80–140 mm FL) were examined for daily bands with a different technique. One sagitta per fish was embedded in epoxy resin and a thick transverse section (>500 µm) was cut. The section was then ground and polished from each side to a level near the core (perpendicular to the long axis of the otolith) by hand with ebony paper (1000 grade) and lapping film (9 and 3 µm). A polished thin transverse section approximately 100 µm thick was produced. The section was then examined with a compound microscope.

Age validation

Marginal increment analysis, routinely used to validate fish age, relies on the assumption that if a translucent zone is laid down once a year, there should be a clear pattern of periodic growth on the edge of the otolith during the year. Marginal increment analysis is appropriate only if all fish in the population lay down the translucent zone at the same time. Thus, an annulus consists of a single opaque and a single translucent cycle within a 12-month period. The opaque zone is believed to form during periods of slow growth.

Marginal increment analysis usually implies measurement of marginal growth and hence many researchers have measured the width of the edge of the otolith section over an annual cycle. This measurement approach has an advantage in that it should be possible to plot growth of the edge over time to validate that only a single translucent mark is laid down each year. However, in *P. multidens*, it can be difficult to determine a consistent location to measure on the otolith because of the inherent variability of their otoliths; hence this technique was not used in the present study.

Edge type analysis was adopted for the marginal increment analysis of *P. multidens* and edge types were classified according to Pearson (1996) as either translucent, narrow opaque (opaque area less than half of the previous opaque zone), or wide opaque (opaque area greater than half of the previous opaque zone). Sectioned otoliths of fish of all ages were examined under a dissecting microscope with reflected light on a black background.

Age determination

Because the peak spawning period of *P. multidens* occurs in late March, all fish were assigned a birth date of 1 April to assure proper year-class identification. Ages were assigned from counts of annual growth increments consisting of alternating opaque and translucent rings from sectioned otoliths (opaque rings were counted). Annual growth increments were counted in the ventral lobe of the otolith from the primordium to the proximal surface, as close as was practicable to the ventral margin of the sulcus acousticus. Annual growth increments were counted without reference to fish length or date of capture. Each otolith section was examined on four separate occasions. When the counts differed, otolith sections were re-examined. In most cases that required resolution, the fourth and final count was used for analysis of age and growth because by this time considerable experience had been gained in the interpretation of the otolith structure. Otoliths with structural irregularities (such as unusual calcification, deterioration of the ventral lobe, or poorly defined annual growth increments) were considered indecipherable and were excluded from analysis of fish age.

Counts were compared and the precision of age estimates were calculated with the average percent error (APE) of Beamish and Fournier (1981). Greater precision is achieved as the APE is minimized. The relationship between fish length (FL) and age and otolith dimensions was assessed with linear regression techniques.

Timing of translucent zone formation in *P. multidens* and mean sea surface temperatures (SST was assumed to reflect the temperature at depth) were compared by scaling values from the two data sets. The scaling process allowed direct comparison of each series and any time lags of one in relation to the other. Using the scaling score = 1 – ((maximum data value – data value) ÷ range), where (in the month of November) mean SST for the month was 29°C, the maximum for the year (data set) was 29.7 and the range of the data values was 3.7, we calculated the scaled *SST* = 1 – ((29.7–29) ÷ 3.7) = 0.81; in addition the scaled % frequency of otoliths with translucent edge types = 1 – ((67–20) ÷ 67) = 0.30.

Growth and mortality models

The von Bertalanffy growth function (VBGF) was fitted to estimates of length-at-age with nonlinear least squares estimation procedures. The VBGF is defined by the equation

$$L_t = L_\infty\left\{1-\exp\left[-K(t-t_0)\right]\right\},$$

where L_t = mean length of fish of age t;
L_∞ = asymptotic mean length;
K = is a rate constant that determines the rate at which L_t approaches L_∞;
t = age of the fish; and
t_0 = the hypothetical age at which the mean length is zero if it had always grown in a manner described by the VBGF.

Table 1

Length-weight relationships for *P. multidens* off the Kimberley coast of northwestern Australia. Estimates were obtained for the parameters a and b of the relationship $W = aL^b$, the sample size (n), and the regression r^2 value (lengths used are fork length [FL] in mm and the weight is total weight [TW] or cleaned weight [CW] in g).

Group	a	b	n	r^2
P. multidens (all fish—TW)	2.483×10^{-5}	2.9501	3680	0.983
P. multidens (all fish—CW)	2.356×10^{-5}	2.9425	3073	0.983
P. multidens (male—TW)	2.156×10^{-5}	2.9737	1963	0.985
P. multidens (female—TW)	2.825×10^{-5}	2.9281	1671	0.987

The von Bertalanffy growth curves for both sexes were compared with the likelihood ratio test of Cerrato (1990).

Estimates of the instantaneous rate of total mortality (Z) were obtained from catch-at-age data from the NDSF. Annual catch in weight was converted to annual catch in numbers-at-age by the use of age-frequency data standardized by fishing effort to obtain catch-per-age class. Catch in weight was converted to catch in numbers based on the mean weight of *P. multidens* observed in the sampled catch each year. Mortality estimates were then derived between successive years by obtaining the natural logarithm of the catch per age class (e.g. age 7) in year t and subtracting the natural logarithm of the catch per age class (e.g. age 8) in year $t + 1$ for all fully recruited age classes. Mean total Z was then calculated across all fully recruited age classes. Instantaneous natural mortality rates (M) were derived by using the general regression equation of Hoenig (1983) for fish, where $\log_e Z = 1.46 - 1.01 \log_e t_{max}$ (t_{max}=the maximum age in years). The Hoenig equation has been shown to provide a reasonable approximation of M in tropical demersal fishes (Hart and Russ, 1996; Newman et al., 1996; 2000b).

The annual percentage removal was estimated by annual percentage = $[F/Z\,(1-e^{-Z})] \times 100\%$. Exploitation rates ($E$) were derived from the estimates of Z and F as defined by the equation $E = F/Z$ (F=the instantaneous rate of fishing mortality derived from the relationship $F=Z-M$). Reference points for target (optimal) and limit fishing mortality rates (F_{opt} and F_{limit}) were calculated for *P. multidens* by using the estimate of natural mortality (M), because $F_{opt} = 0.5\,M$ (Walters, in press) and $F_{limit} = 2/3\,M$ (Patterson, 1992).

Results

A total of 3833 *P. multidens* (ranging in size from 80 to 701 mm FL [10.6–5770 g TW]) were examined for age analysis. Of the fish collected, 2063 were males ranging from 245 to 671 mm FL and from 296 to 5195 g TW, and 1751 were females ranging from 284 to 701 mm FL and from 450 to 5770 g TW. Length conversion equations were derived for total length: $TL = (1.12 \times FL) + 21.84$ (n=2137, r^2=0.995); fork length: $FL = (0.89 \times TL) - 16.61$ (n=2137, r^2=0.995); $FL = (1.12 \times SL) + 6.44$ (n=2148, r^2=0.992); and standard length: $SL = (0.89 \times FL) - 2.14$ (n=2148, r^2=0.992).

Length-weight models

Length-weight relationships were calculated separately for males, females, and for both sexes combined (Table 1). The relationship between TW and FL is presented in Figure 2. ANCOVA of TW-at-FL and CW-at-FL were both significantly different between sexes (TW: F=42.56; df: 1, 3234; P<0.001; CW: F=94.29; df: 1, 2652; P<0.001); males were larger than females. The length-frequency distribution for male and female *P. multidens* is shown in Figure 3.

Temporal trends were evident in the mean length and weight of *P. multidens* over time. Mean FL was significantly different among years from 1995 to 1999 (ANOVA: F=31.29; df: 1, 4193, P<0.001), with (1995=1996=1997) > (1998=1999). Mean TW was also significantly different among years from 1995 to 1999 (ANOVA: F=89.33; df: 1, 3295, P<0.001), with 1995 > 1996 > 1997 > (1998=1999).

Age validation

Otoliths displayed alternating opaque and translucent zones. A consistent annual trend was evident; the translucent zone was laid down from January to May and the opaque zone formed from June to December. The trend in thin opaque zone formation in June and July was replicated in both 1997 and 1998. Figure 4 clearly demonstrates that the opaque and translucent zones are laid down once a year and represent valid annual growth increments. Because the marginal increment analysis involved random sampling across all age classes in the sampled population, the validation of annual growth increments can be expected to hold across all age classes. In addition, the formation of the translucent zone in the sagittal otoliths of *P. multidens* and the annual cycle of sea surface temperatures in the Kimberley region of northwestern Australia were found to be closely related (Fig. 5).

Otolith structure, analysis, and functionality

The sagittae of *P. multidens* are somewhat laterally compressed, elliptical structures. The distal surface is concave and the rostrum and postrostrum are somewhat pointed. The sagittae are characterized by variable growth reticulations along the dorsal edge from the postrostrum to

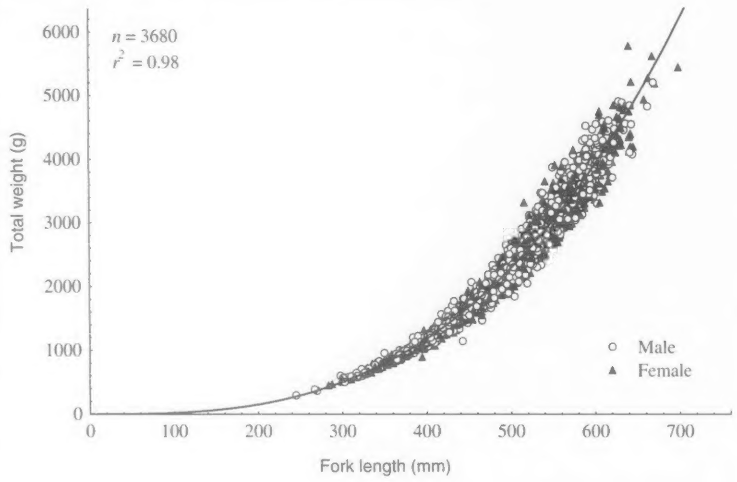

Figure 2

Relationship between fork length and total weight for *P. multidens* off the Kimberley coast of northwestern Australia.

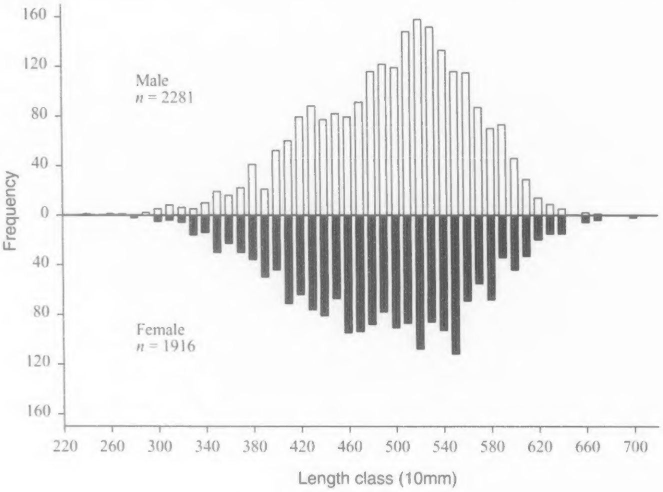

Figure 3

Length-frequency distribution (10-mm length classes) of male and female *P. multidens* sampled for age determination.

the antirostrum and along the ventral edge from the postrostrum to the rostrum. A curved sulcus crosses the proximal surface longitudinally, and the depth of the sulcal groove increases with fish age.

The precision of otolith readings of *P. multidens* was relatively high (APE of 10.4%). Given the variability encountered among otoliths, this APE reflects a moderately high level of precision among otolith readings and indicates that the aging protocol adopted is replicable.

Otolith length and breadth were useful predictors of fish length in *P. multidens*, accounting for more than 77% of the variability (Table 2). In contrast, otolith weight and, in particular, height were poor predictors of fish length (Table 2). Otolith weight was the best predictor of fish age for *P. multi-*

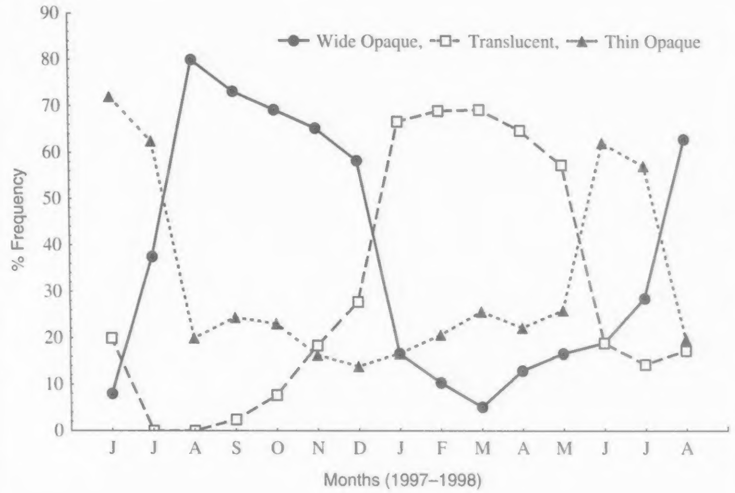

Figure 4

Marginal increment analysis of *P. multidens* sagittal otoliths using an edge type classification system (edge types: wide opaque, thin opaque, and translucent).

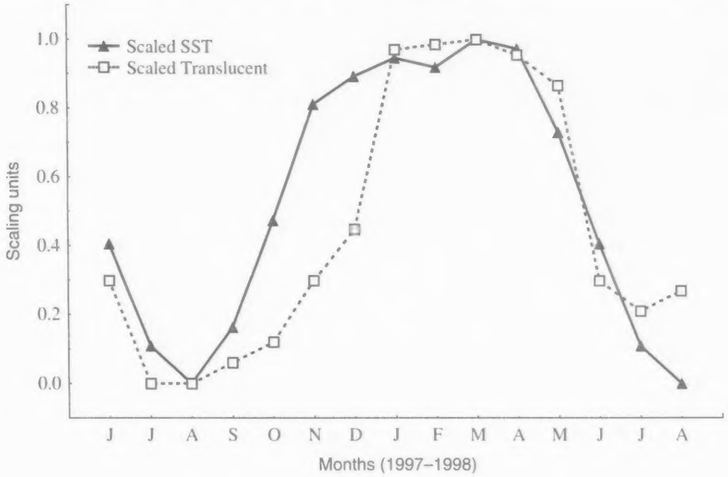

Figure 5

Comparison of the translucent zone formation on the sagittal otoliths of *P. multidens* with sea surface temperatures in the Kimberley region of northwestern Australia. Values are standardized to take into account any time lags and to allow comparison of each time series.

dens, accounting for 94.4% of the variability in age (Table 2, Fig. 6). Otolith height was also a useful predictor of fish age, accounting for 88% of the variability in age. In contrast, otolith length and breadth were poor predictors of age for *P. multidens* (Table 2).

Growth and mortality models

The von Bertalanffy growth curve was fitted to FL-at-age for all *P. multidens* (Fig. 7), and separately for each sex (Table 3). Growth in FL of *P. multidens* is relatively fast to

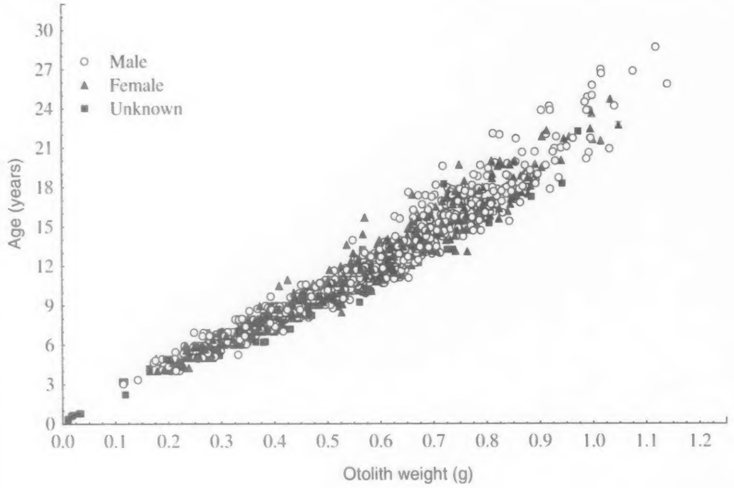

Figure 6

Relationship between otolith weight and age of *P. multidens* estimated from sectioned otoliths.

Table 2

Comparisons among otolith dimensions and length and age of *P. multidens*. The predictive equations are of the simple linear regression form $y = a + bx$ (OW=otolith weight; OL=otolith length; OB= otolith breadth; OH=otolith height). For regression analyses, fish length (FL) and age were used as the dependent variables (all regressions were significant at $P<0.001$). The standard error (SE) of the estimate is a measure of the dispersion of the observed values about the regression line.

Dependent variable	Independent variable	Sample size	Equation	r^2	SE of estimate
FL	*OW*	2590	$FL = (315.37 \times OW) + 339.46$	0.68	37.57
FL	*OL*	2493	$FL = (33.47 \times OL) - 111.43$	0.77	32.08
FL	*OB*	3745	$FL = (50.43 \times OB) - 124.36$	0.83	28.48
FL	*OH*	3988	$FL = (118.39 \times OH) + 175.14$	0.53	48.36
Age	*OW*	2408	$Age = (21.86 \times OW) - 0.68$	0.94	0.94
Age	*OL*	2305	$Age = (1.77 \times OL) - 21.68$	0.58	2.63
Age	*OB*	3469	$Age = (2.40 \times OB) - 19.14$	0.60	2.49
Age	*OH*	3652	$Age = (8.52 \times OH) - 12.81$	0.88	1.36

age 9 but is much reduced in age cohorts beyond 9 years of age. Parameters of the VBGF are listed in Table 3. FL-at-age of *P. multidens* was not significantly different between sexes (log-likelihood=0.9836, test statistic=1.001, $P>0.05$; no significant differences were found among parameters of the VBGF; see also Fig. 7). Generalized VBGFs of *P. multidens* from previous studies were compared to that derived from our study (Fig. 8).

The maximum observed age of *P. multidens* in the Kimberley region was 30 years. Given that the *P. multidens* resource in the Kimberley region has been exploited for over 20 years, it is possible that in an unfished population the longevity of *P. multidens* may be closer to 40 years. These two estimates of maximum age in *P. multidens* were applied to the Hoenig (1983) equation in order to derive an estimate of *M*. Consequently, *M* was considered to be in the range of 0.104–0.139, representing an annual survivorship of 87–90% for an unfished population. This range of *M* estimates for *P. multidens* is similar to that observed for other long-lived lutjanid species in the Indo-Pacific region (Newman et al., 1996, Newman et al., 2000a; Newman and Dunk, 2002).

The longevity of female and male *P. multidens* was somewhat similar at 27 and 30 years, respectively. The age structures of *P. multidens* in the commercial catch differed among years. The 1995 sample had a peak in year

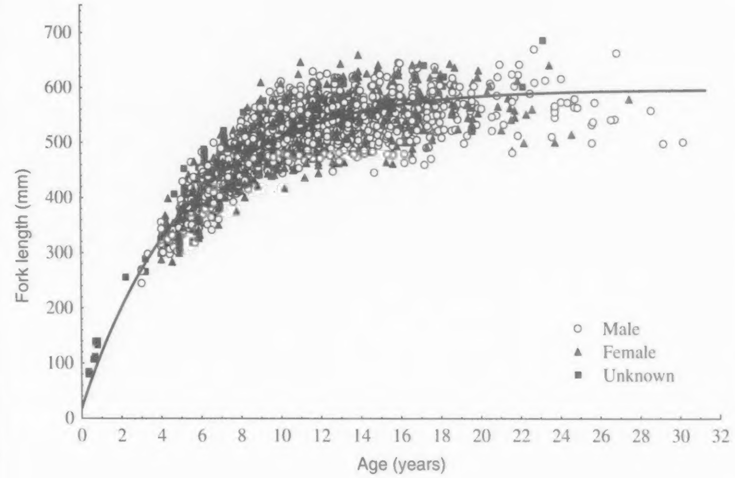

Figure 7

Length-at-age and von Bertalanffy growth curve for *P. multidens* off the Kimberley coast of northwestern Australia.

class 5 and relatively strong age classes 6, 8, and 10, but abundance per age class declined rapidly to age 20, after which few fish were found to be older (Fig. 9). The 1996 and 1997 samples were somewhat similar. In 1996 relatively strong year classes were present from age 5 through to age 11, and abundance per age class declined rapidly to age 26 (Fig. 9). One year later, the 1997 sample had relatively strong year classes present from age 6 through to age 12 (Fig. 9), providing further evidence of the annual formation of growth increments.

The 1998 sample had relatively strong 6, 7, and 8 age classes, and abundance per age class declined rapidly to age 24 (Fig. 9). The 1999 sample was similar to the 1998 sample with relatively strong 6, 7, and 8 age classes, and abundance per age class declined rapidly to age 20 (Fig. 9). Age classes 9 through 12 were somewhat eroded in the 1998 and 1999 samples in comparison to the 1996 and 1997 samples. In all years, abundance per age class declined rapidly to age 20, and fish older than 20 years were not well represented in the catch over the five years of catch sampling. In most years there was a strong mode of age-6 individuals present and this mode may reflect the age at full recruitment to the sampling gear (fish traps).

Pristipomoides multidens less than age 6 were in general not fully recruited to the sampled population and were therefore excluded from the mortality estimates derived from catch-at-age data. The year-specific total annual rate of mortality, Z, of *P. multidens* in the NDSF, was 0.65 for 1995–96 (fish aged 6–21 years), 0.87 for 1996–97 (fish aged 6–21 years), and 0.71 for 1997–98 (fish aged 6–21 years), representing an annual percentage removal of approximately 38%, 49%, and 41%, respectively, for each year (Table 4). In addition, exploitation rates were 0.79, 0.84, and 0.80, respectively.

Table 3

Growth parameters derived from the von Bertalanffy growth function and population characteristics of *P. multidens* off the Kimberley coast of northwestern Australia (n=sample size, FL is in mm, and age (t) is in years).

Parameters	Male	Female	Total
n	1879	1600	3479
L_∞	594.49	603.23	598.08
K	0.1868	0.1867	0.1873
t_0	−0.3601	0.0018	−0.1730
r^2	0.7394	0.7875	0.7630
n	2281	1916	4573
FL_{mean}	501.5	493.5	495.1
FL_{min}	245	284	80
FL_{max}	671	701	701
n	1872	1597	3833
t_{mean}	10.24	9.54	9.73
t_{min}	3	4	0.35
t_{max}	30	27	30

The optimum fishing mortality rate, F_{opt}, for *P. multidens* was estimated to be 0.052–0.069, and the limit reference point, F_{limit}, was estimated to be 0.069–0.092 (see Table 4). These results indicate that only approximately 6% of the

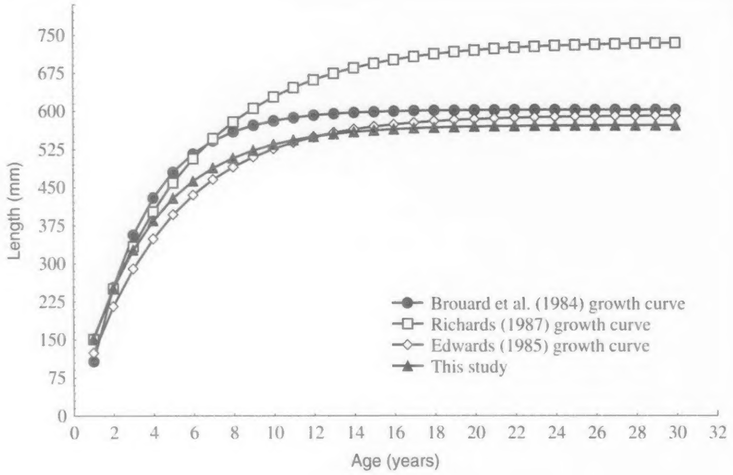

Figure 8

Comparison of generalized von Bertalanffy growth curves for *P. multidens* from previous studies with that derived from this study.

Table 4

Summary of total mortality (Z) estimates for *P. multidens* derived from catch-at-age data based on ages determined from sectioned otoliths. Estimates of fishing mortality (F) are derived by subtraction because $Z = F + M$ and are compared to estimates of optimum fishing mortality rates.

Year	Z	F	F_{opt}	F_{limit}
1995–96	0.649	0.510–0.545	0.052–0.069	0.069–0.092
1996–97	0.869	0.730–0.765	0.052–0.069	0.069–0.092
1997–98	0.710	0.571–0.606	0.052–0.069	0.069–0.092

available stock of *P. multidens* can be harvested on an annual basis in a sustainable manner and that annual harvest rates should not exceed 10% of the average stock size.

Discussion

Sagittal otoliths were determined to be valid structures for age determination in *P. multidens*. The edge-type classification system of three edge types used in this study is capable of indicating whether the opaque zone has just been formed or whether a new translucent zone is ready to form. The use of marginal increment analysis (MIA) of individuals of all ages exhibits a clear trend and demonstrates conclusively that annual growth increments are formed once per year. Annual growth increments were most conspicuous in the ventral lobe of the sagittal otoliths. However, we observed that experience is a critical factor in increasing the agreement and hence precision of successive counts of annual growth increments in *P. multidens*.

The spring–summer peak in opaque zone formation observed in our study is in accordance with the peak in opaque zone formation identified by Fowler (1995) and Beckman and Wilson (1995) for tropical fishes. The translucent zone (the period of fast growth in the otoliths) is formed in the summer months (January to May) and the opaque zone (the slow growth period) is formed in the winter-spring months (June to December). Translucent zones are relatively thin. Declining sea-surface temperature (which was assumed to reflect water temperature change at depth) was associated with the onset of opaque zone formation in the otoliths of *P. multidens*. Furthermore, reproduction is unlikely to play a significant role in the timing of translucent zone formation in *P. multidens* because spawning occurs primarily in the March–April period. These results indicate that water temperature, doubtless in association with other factors, provides a stimulus that influences the endolymph fluid chemistry of these fish, culminating in the formation of annual growth increments.

Female and male fish older than 20 years of age were uncommon in the landed catch. Fish of both sexes between 5 and 12 years of age were common in the landed catch. The maximum age of *P. multidens* observed in our study was much greater than that recorded previously. Richards[1] reported a maximum age of 14 years in Papua New Guinea from counts of daily rings on otoliths, whereas Brouard et al. (1984) recorded a maximum age of only 8 years in Vanuatu with a similar method. Edwards (1985) analyzed vertebrae and scales of this species in the Timor Sea and reported a maximum age of 14 years. In contrast, Mohsin and Ambak (1996) estimated a maximum age of only 5 years from the east coast of peninsular Malaysia with length-frequency analysis. Variation in the longevity estimates of earlier works is related to the aging methods used and their biases. For example, growth increments in vertebrae are often difficult to detect despite the presence of numerous discontinuities in bone growth (Marriott and Cappo, 2000). Alternatively earlier longevity estimates may have been drawn from sample populations biased by gear selectivity or from populations with varying degrees of exploitation.

Otolith weight was a good predictor of age in *P. multidens*, accounting for 94% of the variability in age. The strong linear relationship between otolith weight and fish age from a very large sample size implies that otolith weight may be used as a proxy for age. The coefficient of determination of the regression model is affected by the degree of colinearity of the independent variables. The high r^2 value observed in our study provides the basis for a first-order age approximation. Thus, the potential exists for an age–otolith-weight key to be derived for *P. multidens*, as for an age-length key, whereby the age composition of the landed catch in future years may be obtained by weighing large numbers of otoliths. However, the accuracy and precision of adopting this monitoring strategy remains to be tested.

The fit of the regression model for the otolith weight-age relationship was much more precise than the fit of the fork-length–age relationship as described by the von Bertalanffy growth model. Considerable variation in length was observed within most age groups for both sexes. The large variation in length at a given age makes it difficult to accurately determine the age of *P. multidens* from length data alone. For example, fish ranging in length from 450 to 550 mm FL may vary in age from 5 to 30 years. This variability may explain the very low estimate of maximum age obtained by Mohsin and Ambak (1996), which was derived with length-frequency analysis.

Growth was most rapid through age 9 for both sexes. From age 9 onwards somatic growth slows with increasing age. The estimation of growth parameters is dependent upon adequate sampling across the length range of any species. The fish sampled in our study ranged in length from 80 to 701 mm FL, covering most of the length range of *P. multidens*. Therefore, it is unlikely that the growth parameters of *P. multidens* are biased because of inadequate sampling across the length range.

Despite methodological differences in age estimation, the estimates of *K* derived from the studies of Richards[1]

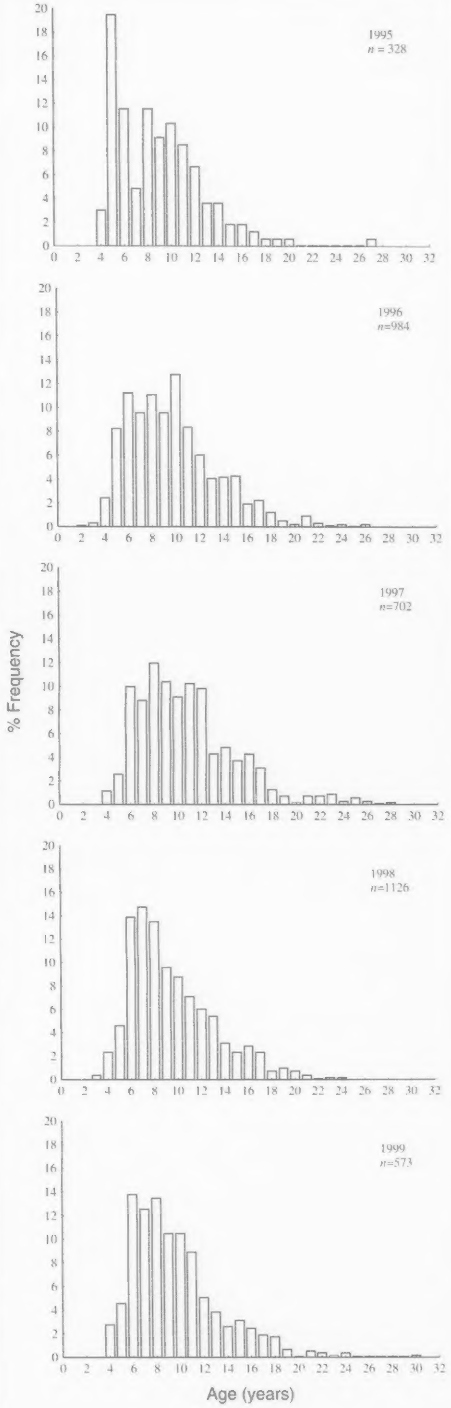

Figure 9

Age-frequency distributions of *P. multidens* in the northern demersal scalefish fishery from 1995 to 1999.

(K=0.188), Ralston (1987; K=0.188), and Edwards (1985; K=0.219) were somewhat similar to that observed in this study (K=0.187). However, the asymptotic lengths reported by Richards[1] and Ralston (1987) were larger than our estimates, which were again similar to those of Edwards, 1985). In contrast, the estimates of K derived by Brouard et al. (1984), Brouard and Grandperrin (1985), and Mohsin and Ambak (1996), which ranged from 0.28 to 0.50, provided overestimates of the growth potential of *P. multidens* as observed in our study. Clearly, methodological differences in age estimation have the potential to unduly influence growth parameter estimation and may provide misleading impressions of the production potential of these fishes.

The similarity of growth in length-at-age between sexes indicates that there is little trade off in energetic investment into reproductive activity after sexual maturity at the expense of somatic growth as there is for some *Lutjanus* species (Newman et al., 1996, 2000b). Information on energy partitioning in the *Pristipomoides* is not known. However, females with a large body size would be reproductively "fitter" if they could accommodate a large mass of hydrated eggs prior to spawning, especially in a multiple male, multiple female spawning system.

The long life span of *P. multidens* and other lutjanid species (Loubens, 1980; Newman et al., 1996, 2000a; Newman and Dunk, 2002; Rocha-Olivares, 1998) may be an evolutionary adaptation that supports iteroparity. Many demersal reef fish are highly fecund, but egg and larval survivorship is low; therefore, spawning over numerous years may be necessary to maintain stable populations. In addition, numerous years of reproductive output may also be required to contend with environmental variability (e.g. the incidence of cyclones, El Niño–La Niña cycling), which may substantially influence recruitment success. Extended periods of high exploitation results in decreases in the spawning stock biomass and constriction of the age structure of fish populations, and thus diminishes the number of effective spawnings. Any reduction in the number of effective spawnings may result in a decrease in ecological fitness and hence limit the adaptive capacity of the species to combat environmental or anthropogenic induced stress.

Variation in life expectancy due to fishing pressure has the potential to bias estimates of M used in our study. To account for any M-associated difference, a range of M estimates have been considered in our study. *Pristipomoides multidens* were fully recruited to the commercial fishery in the NDSF by age 6. Catch-at-age data showed relatively consistent estimates of Z among years from 1995–96 through to 1997–98 and a relatively broad age structure in the landed catch.

Fishery management implications

Throughout much of its range *P. multidens* composes a significant proportion of the demersal catch of tropical multispecies fisheries. Within these multispecies fisheries *P. multidens* is taken as part of the directed target catch or as a part of the retained catch. In fish trawl-based fisheries, *P. multidens* can be harvested at all stages of their life history from juvenile to adult, making them especially vulnerable to overexploitation. In contrast, fisheries that use trap and line methods of capture (using bait to attract fish) only have the capacity to harvest fish in the subadult-to-adult phase of their life history. Hence, the method of capture and harvest strategy adopted has the capacity to influence the sustainable exploitation of the *P. multidens* resource.

Of particular relevance to fishery managers is the capacity that fish trawl-based fisheries have in being capable of continuing to function and to be economically viable (driven by the more productive, lower value species) while populations of higher valued species such as *P. multidens* become depleted. Thus, careful monitoring of the *P. multidens* resource will be required, particularly in trawl-based fisheries. Fishery managers need to be responsive to the intrinsic vulnerability of *P. multidens* to overharvesting as a corollary of its life history characteristics. Furthermore, fish such as *P. multidens*, which have low rates of natural mortality, low growth potential, extended longevity, mature relatively late in life and are either dead or moribund as a consequence of internal hemorrhaging when the physoclistous is ruptured during capture, are likely to be particularly sensitive to exploitation pressure. The apparent low survival rate for released fish in the fishing depths of the NDSF fleet indicates that the traditional use of legal minimum sizes to increase survival to spawning sizes and hence increase overall yields is not a practical option.

Populations of *P. multidens* have a low productive capacity and hence are vulnerable to overfishing as a consequence of slow growth, extended longevity, late maturity, and low rates of natural mortality. The demersal fish resources of the NDSF, of which *P. multidens* is a significant part, is currently being managed with an innovative total allowable effort system that allocates individually transferable effort units equitably to each licensee. However the highly mobile, efficient, and wide-ranging capacity of the NDSF fleet may require more complex management arrangements to maintain future breeding stock levels. The incorporation of appropriately targeted spatial or temporal (or both spatial and temporal) closures within the existing effort management framework is likely to provide an additional useful and robust mechanism to maintain spawning stock biomass and protect against recruitment overfishing. In the wider Indo-Pacific region, fishery managers should consider harvest strategies of low frequency or low intensity in conjunction with targeted spatial or temporal closures to protect the spawning stock biomass of these fishes.

Harvest strategies such as setting fishing mortality at or near natural mortality (F=M) were often prescribed prior to the 1990s (Gulland, 1970). Recently, the adoption of harvest strategies such as setting $F = F_{0.1}$ were thought to be quite conservative, but usually resulted in $F = M$ harvest strategies (Walters, in press). Following the meta-analysis of Myers et al. (1999), who examined stock-recruitment curve slopes expressed as maximum reproductive rates per spawner at low spawner biomass, Walters (in press) has reported that optimal fishing mortality rates are substantially lower than natural mortality rates for most species and stocks. Furthermore, Patterson

(1992) reported that fishing mortality rates above 2/3 *M* are often associated with stock declines, whereas fishing mortality rates below this level have resulted in stock recovery. Consequently, exploitation rates for long-lived reef fishes need to be very conservative.

The declines evident in the length and weight of fish in the landed catch over the duration of our study support the finding of the high levels of *F*. These data support the estimates of the annual percentage removals that indicate that the NDSF population of *P. multidens* is currently exploited above optimum levels. The age structure of the *P. multidens* stock within the NDSF currently consists of close to 30 age classes (ages 2 to 30 years). Therefore, depletion of the spawning stock biomass of these fishes will result in long population recovery times and the economic loss associated with recovering and rebuilding these fisheries may persist longer. A minimum of 30 years would be required for the fished population to recover in terms of both virgin spawner biomass and age structure. The results of our study provide the basis for a more detailed age-structured stock assessment for this species.

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An approach to estimating rockfish biomass based on larval production, with application to *Sebastes jordani**

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Abstract—An assessment of the total biomass of shortbelly rockfish (*Sebastes jordani*) off the central California coast is presented that is based on a spatially extensive but temporally restricted ichthyoplankton survey conducted during the 1991 spawning season. Contemporaneous samples of adults were obtained by trawl sampling in the study region. Daily larval production (7.56×10^{10} larvae/d) and the larval mortality rate (Z=0.11/d) during the cruise were estimated from a larval "catch curve," wherein the logarithm of total age-specific larval abundance was regressed against larval age. For this analysis, larval age compositions at each of the 150 sample sites were determined by examination of otolith microstructure from subsampled larvae (n=2203), which were weighted by the polygonal Sette-Ahlstrom area surrounding each station. Female population weight-specific fecundity was estimated through a life table analysis that incorporated sex-specific differences in adult growth rate, female maturity, fecundity, and natural mortality (M). The resulting statistic (102.17 larvae/g) was insensitive to errors in estimating M and to the pattern of recruitment. Together, the two analyses indicated that a total biomass equal to 1366 metric tons (t)/d of age-1+ shortbelly rockfish (sexes combined) was needed to account for the observed level of spawning output during the cruise. Given the long-term seasonal distribution of spawning activity in the study area, as elucidated from a retrospective examination of California Cooperative Oceanic Fisheries Investigation (CalCOFI) ichthyoplankton samples from 1952 to 1984, the "daily" total biomass was expanded to an annual total of 67,392 t. An attempt to account for all sources of error in the derivation of this estimate was made by application of the delta-method, which yielded a coefficient of variation of 19%. The relatively high precision of this larval production method, and the rapidity with which an absolute biomass estimate can be obtained, establishes that, for some species of rockfish (*Sebastes* spp.), it is an attractive alternative to traditional age-structured stock assessments.

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Fish. Bull. 101:129–146 (2003).

Shortbelly rockfish (*Sebastes jordani*) is an underutilized species that is distributed from Vancouver Island to northern Baja California (Eschmeyer, 1983), although it is especially abundant along the central California coast. Based on a swept-area bottom trawl survey of demersal rockfish, Gunderson and Sample (1980) estimated there were 24,000 metric tons (t) of shortbelly rockfish in the Monterey International North Pacific Fishery Commission (INPFC) area (35°30′N–40°30′N). This biomass estimate was far greater than that of any other species of rockfish in any area and, significantly, it did not include the midwater portion of the stock. Hydroacoustic estimates of shortbelly rockfish biomass in the shelf-slope area between Ascension Canyon and the Farallon Islands (37°00′–38°00′N), a distance of only 110 km, have ranged from 153,000 to 295,000 t (Nunnely[1]).

Although at present there is no directed fishery for this species (Low, 1991), much is known of its biology. Early work by Phillips (1964) provided basic information about the length-weight relationship, growth as estimated from scale annuli, spawning seasonality (i.e. parturition), fecundity, maturity, and the food habits of shortbelly rockfish. Lenarz (1980) later studied shortbelly rockfish growth using ages from whole otoliths and provided preliminary calculations of the effect of fishing on the stock. He also demonstrated marked spatial variation in age and length composition along both latitudinal and depth gradients. Growth was re-estimated by Pearson et al. (1991) using ages determined from broken and burnt otoliths. From the hydroacoustic biomass estimates cited above and an estimated range for the natural mortality rate (0.20–0.35 yr), they concluded that the maximum sustainable yield (MSY) of the shortbelly rockfish stock in the Ascension Canyon–Farallon Islands area was 13,400–23,500 t.

Shortbelly rockfish is one of the few *Sebastes* spp. that can be readily identified at all life history stages. Descriptions of the early life stages of shortbelly rockfish, from preflexion larvae through the pelagic juvenile stage, were provided by Moser et al. (1977). Extending that work, MacGregor (1986) provided a summary of the spatiotemporal distributions of shortbelly rockfish larvae taken in California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises conducted in five different years. His results showed that 99.1% of all shortbelly rockfish larvae (~4–10 mm) were captured within 90 km of shore and that 65.4% were sampled during the month of February. Moreover, a strong peak in larval abundance (i.e. 34.7% of the coastwide total) was concentrated in the vicinity of Pioneer Canyon (CalCOFI line 63). Later research by Laidig et al. (1991) resulted in the development of a detailed growth model for young-of-the-year shortbelly rockfish, from extrusion through the late pelagic juvenile stage (~180 d), and verified the feasibility of a daily aging protocol by validating a one-to-one correspondence between counts of daily increments and elapsed time in days. More recent work by Ralston et al. (1996) showed that larval shortbelly rockfish can be accurately aged by using optical microscopy.

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[1] Nunnely, E. 1989. Personal commun. Alaska Fisheries Science Center, 7600 Sand Point Way N.E., Bin C15700, Seattle, WA 98115-0070.

For the year 2000 the Pacific Fishery Management Council (PFMC) revised the shortbelly rockfish acceptable biological catch (ABC) downwards from 23,500 to 13,900 t/yr (PFMC[2]). The new ABC is based on the low end of the estimated MSY range presented in Pearson et al. (1991); it was reduced due to a probable natural decline in standing stock during the 1990s arising from poor ocean conditions (MacCall, 1996). The original range, however, was derived by using quite variable data from unpublished hydroacoustic surveys and Pearson et al. (1991) considered it a strictly preliminary estimate. Given that the biomass of shortbelly rockfish along the central California coast was once thought to be very large (Gunderson and Sample, 1980; MacGregor, 1986), and that the species is still probably the single largest rockfish contribution available to the west coast groundfish fishery, data are needed to estimate the size of the stock more precisely than results available from these previous investigations.

The goal of this study was to develop an analytical approach to estimate the total biomass of shortbelly rockfish in the region of Pioneer and Ascension Canyons and to gather field data to evaluate the method. Successful application of the method to shortbelly rockfish would provide to the PFMC information useful for management. On a more fundamental level, it would also assist in developing fishery-independent survey techniques capable of assessing other, more highly exploited, species of rockfish.

The assessment approach

The basic premise of egg and larval surveys is that it is easier to estimate the absolute abundance of ichthyoplankton than it is to estimate that of adults (Saville, 1964; Gunderson, 1993). This is especially true when the spatial distribution of adults exhibits some type of size- or age-specific pattern. Shortbelly rockfish is one such species (Lenarz, 1980) and obtaining a representative sample of the adult population is challenging (Lenarz and Adams, 1980). Conversely, early life history stages (i.e. eggs and preflexion larvae) can be sampled effectively with standard plankton nets (Smith and Richardson, 1977). Due to the direct coupling between egg production and spawning biomass, mediated through population weight-specific fecundity(Φ[eggs/g]), egg and larval surveys have proven successful for estimating spawning biomass in many applications (e.g. Houde, 1977; Parker, 1980; Richardson, 1981; Lasker, 1985; Armstrong et al., 1988; Hunter et al., 1993).

Members of the scorpionfish genus *Sebastes* are distinctive because they are primitive viviparous livebearers (Wourms, 1991), resulting in parturition of advanced yolksac larvae (Bowers, 1992). This reproductive strategy lends itself to a larval production stock assessment because the age of all spawning products can be accurately determined from otolith microstructure (Laidig et al., 1991; Ralston et al., 1996). In contrast, in egg surveys, egg age is back-calculated to the time of spawning by 1) defining a series of developmental stages, 2) estimating the relationship between stage-specific developmental rates and temperature, 3) assigning a thermal history to each egg, and 4) determining the time required to account for embryo development from spawning to the observed stage (see for example Lo, 1985; Moser and Ahlstrom, 1985). Because a distinctive extrusion check forms on the otoliths of *Sebastes* larvae at the time of parturition (Ralston et al., 1996), a rockfish larval production estimate does not require information on temperature-dependent developmental rates and the ambient thermal history of egg samples.

In the approach presented in the present study, a spatially extensive but temporally restricted ichthyoplankton survey was conducted. The age composition of larvae in each plankton tow was determined by subsampling the catch, aging the subsample, and expanding the subsample age composition back to that of the tow total. The total age-specific abundance of larvae in the study region was calculated by weighting the larval catch-at-age in each plankton sample by the polygonal area around it (see Sette and Ahlstrom, 1948). Characterization of the declining trend in total larval abundance at age with an exponential mortality model allowed estimation of the production rate of day-0 larvae and the larval mortality rate at the time the ichthyoplankton cruise was conducted.

Information on adult reproduction was obtained from contemporaneous data collected during two separate cruises conducted during the spawning season. In particular, the following functional relationships were estimated from the data collected: 1) weight as a function of total length, 2) sex-specific weight at age (i.e. male and female von Bertalanffy growth equations), 3) fecundity as a function of total weight, 4) maturity as a function of age, and 5) the population sex ratio. From these relationships, a life table was constructed, based on an estimate of natural mortality (/yr), that yielded estimates of population weight-specific fecundity (Φ). As defined here, population weight-specific fecundity includes the biomass contributions to total population size from males and immature females.

Together, these estimates (daily larval production and population weight-specific fecundity) can be used to calculate the "daily" total biomass of fish in the population required to produce the observed abundance of larvae. The long-term mean seasonal distribution of shortbelly rockfish larvae and spawning activity was then determined by a retrospective analysis of all CalCOFI ichthyoplankton samples collected in the vicinity of Pioneer Canyon. Based upon the timing of our larval survey with respect to the long-term mean distribution of spawning activity, total "annual" biomass was calculated by expansion. Finally, the robustness of the total biomass estimate was evaluated through a simulation study and sensitivity analyses.

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[2] PFMC (Pacific Fishery Management Council). 1999. Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000, 44 p. + 54 tables and 5 figs. Pacific Fishery Management Council, 2130 SW Fifth Ave., Portland, OR 97201.

Methods

Trawl sampling of adults

Specimens of adult shortbelly rockfish were collected during February–March 1991 by the FV *New Janet Ann* and the RV *Novodrutsk* (Table 1). Shortbelly rockfish aggregations in and around Ascension and Pioneer Canyons (Fig. 1) were targeted from acoustic surveys. A total of 28 trawls (12 bottom and 16 midwater) were conducted over bottom depths ranging from 115 to 384 m, at an average net depth of 126 m (range: 18–210 m). The bottom trawl codend mesh size was 3.8 cm and the midwater trawl mesh was 5.1 cm. Duration of the trawls ranged from 3 to 73 min ($\bar{x}$=26 min). All landings were either fully weighed or subsampled, depending on the size of the catch. Landings were highly variable, ranging from 23 to 36,300 kg.

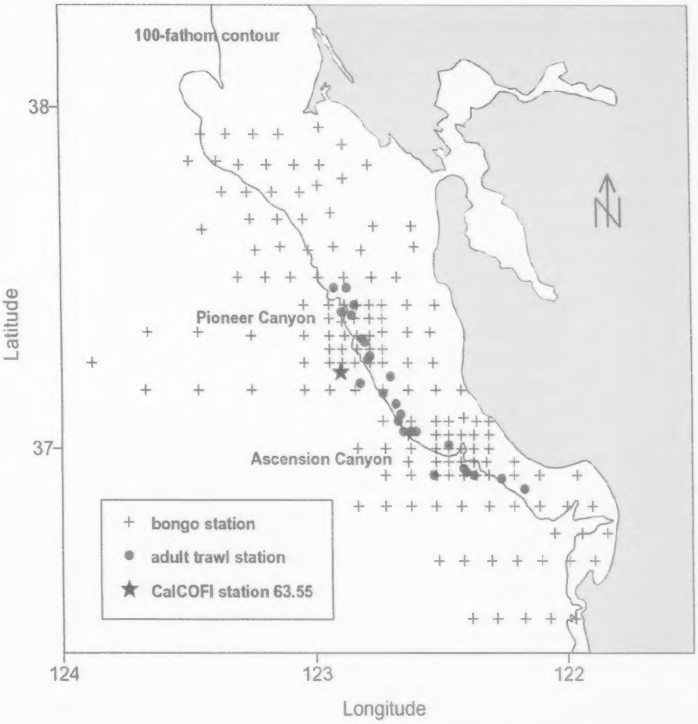

Figure 1

Map of the central California study region showing bongo net and adult trawl sampling locations. The annual spawning season was estimated by the long-term seasonal distribution of shortbelly rockfish larvae at CalCOFI station 63.55.

Two subsamples were taken from each trawl landing. The first was used to determine the overall age, size, sex, and maturity composition of the catch; it was obtained by randomly selecting and examining 100–300 individuals from each trawl, depending on the availability of both time and fish. For these specimens, total lengths (TL) were measured to the nearest mm, gonads were examined to determine sex and to assign gross maturity stages (see below), and otoliths were removed for later age determination by the break-and-burn method (Pearson et al., 1991). A second smaller subsample of 25–50 specimens was also taken to estimate length-weight and fecundity relationships. For each of these fish, TL was measured, weight was determined to the nearest mg, the otoliths were extracted, and late vitellogenic ovaries were dissected from females and fixed in Gilson's fluid.

We rated females in terms of maturity based on gross gonadal condition. A summary of the scale we used is the following: 1.0 = immature; 2.0–2.9 = vitellogenic oocytes (yolk deposition with associated oocyte and ovary enlargement); 3.0–3.9 = fertilized eggs (embryos to hatched larvae); 4.0 = spent; and 5.0 = reorganization and recovery.

Table 1

Summary information of trawl collections for adults. Trawl locations are shown as closed circles in Figure 1. NJA = RV *New Janet Ann*; NOV = RV *Novodrutsk*.

		Trawl type	
Date	Vessel	Bottom	Midwater
14 Feb 1991	NJA	3	1
15 Feb 1991	NJA	2	1
22 Feb 1991	NJA	4	1
23 Feb 1991	NJA	3	1
15 Mar 1991	NOV	0	3
16 Mar 1991	NOV	0	3
17 Mar 1991	NOV	0	2
18 Mar 1991	NOV	0	2
19 Mar 1991	NOV	0	2

Fecundity of female shortbelly rockfish was estimated gravimetrically from vitellogenic ovaries after 2–4 months fixation with periodic stirring. Entire fixed ovaries from each female were blotted dry and weighed to the nearest 1.0 mg. Duplicate subsamples of both ovaries were weighed to the nearest 0.1 mg and their egg contents counted with the aid of a dissecting microscope. The mean number of eggs per gram from each fish was then expanded to the total ovary weight to estimate annual fecundity (total eggs per individual female).

To estimate population weight-specific fecundity, first the length and weight data were fitted to the power function and the bias-corrected regression equation was used to estimate the weight of every fish that was aged. Next, for each sex, growth equations were obtained by fitting the weight and age "data" to the von Bertalanffy growth model (Ricker, 1975). Maturity was quantified by fitting the logistic equation to the proportion of females that were mature within 5-mm-TL intervals, and fecundity was estimated by fitting fecundity and female weight data to the power function, with appropriate bias-correction. These various functional relationships were then combined in a life table analysis to determine the expected biomass per female recruit and the expected lifetime larval production per female recruit. The ratio of these quantities is the estimated equilibrium cohort weight-specific fecundity (i.e. Φ[larvae/g]) of female shortbelly rockfish. Given an estimate of total age-0 larvae (N_0), the female biomass responsible for the observed larval production can be estimated as $N_0\Phi^{-1}$. Finally, the combined sex biomass can be determined by expanding female biomass using weight-based cohort sex ratio estimates from the life table analysis.

Ichthyoplankton sampling

The primary set of ichthyoplankton samples used in our study was obtained by using bongo nets during a cruise of the NOAA RV *David Starr Jordan* (DSJ-9102) conducted in the winter of 1991. Sampling began at 1500 h on 8 February and ended at 0230 h on 15 February. During that 6½-day period 150 stations were occupied in the region bounded from lat. 36°30′N to lat. 38°00′N and offshore to a maximum distance of 130 km (Fig. 1). The study area included Pioneer and Ascension Canyons—two features in the continental slope known to harbor large numbers of adults (Lenarz, 1980; MacGregor, 1986; Chess et al., 1988). At these sites the sampling density was increased.

Field and laboratory processing of the bongo net samples followed prescribed CalCOFI guidelines (i.e. Kramer et al., 1972; Smith and Richardson, 1977), with minor modification. For example, at every fifth sampling station, the bongo frame was deployed with 333-µm and 505-µm mesh nets to determine the extent of extrusion of small larvae in the standard 505-µm mesh (Lenarz, 1972; Somerton and Kobayashi, 1989). After the nets were washed down, samples from both mesh sizes were preserved in 80% EtOH. At all other stations, the net frame was deployed with two 505-µm mesh nets; one sample was preserved in 80% EtOH (to allow later age determinations from larval otoliths), and the other was preserved in 10% buffered formalin. In addition, because *Sebastes* larvae were believed to occur only in the upper mixed layer (Ahlstrom, 1959), the maximum amount of wire deployed was 200 m, resulting in a maximum depth fished equal to 140 m. Following splitting, sorting, identification, and enumeration of the larvae in the laboratory, abundance was expressed as the number of shortbelly rockfish per 10 m^2 of sea surface.

To estimate the age composition of the larval population, the sorted shortbelly rockfish larvae from each of the 150 EtOH-preserved bongo hauls were randomly subsampled for otolith microstructure examination. To determine the size of an age subsample (N_s), based upon the total number of larvae occurring in a haul (N_h), we applied the following rule: 1) for N_h less than or equal to 10, $N_s = N_h$, 2); for N_h greater than 10 but less than or equal to 410, $N_s = 10 + 0.10[N_h - 10]$; and 3) for N_h greater than 410, $N_s = 50$. Otoliths were extracted from each specimen in the haul subsample and individual ages determined by methods outlined in Laidig et al. (1991) and Ralston et al. (1996).

The age composition of the larvae in each bongo sample was then estimated by expanding the percent age-frequency obtained from the subsample to the haul total (N_h). The estimated numbers-at-age of larvae in each haul were standardized to the number per 10 m^2 of sea surface (n_{Ti} for age T and haul i) by application of standard haul factors (Kramer et al., 1972; Smith and Richardson, 1977).

We expanded the n_{Ti} to the entire survey area by using the method of Sette and Ahlstrom (1948). The Sette-Ahlstrom estimate is calculated by the following equation (see Kendall and Picquelle, 1990):

$$\hat{N}_T = \sum_{i=1}^{k} A_i \times n_{Ti},$$

where for each of k hauls A_i = the area that haul i represents (units of 10 m^2); and
N_T = the total abundance of larvae of age T in the entire survey area.

The area for a haul (A_i) is defined as the area circumscribed by a polygon containing all points in space closer to a haul's location than to the location of any other haul. With this definition, we were able to write a simple computer program to calculate Sette-Ahlstrom weights by dividing the study area into a fine grid and assigning each grid point to a haul. Note that this definition and procedure for obtaining Sette-Ahlstrom areas is equivalent to constructing polygons manually using perpendicular bisectors and measuring their areas (Sette and Ahlstrom, 1948).

The mean daily larval production rate during the cruise was estimated as the bias-corrected antilogarithm of the y-intercept of the ordinary least-squares linear regression of $\log_e[N_t]$ against larval age. Moreover, the regression slope provides an estimate of the total instantaneous mortality rate of the larvae (Z [/d]). This calculation implicitly assumes that the age distribution of larvae was stationary throughout the 6½-day period of the cruise.

To determine if shortbelly rockfish larvae occur deeper in the water column than 140 m, a series of 1-m^2 multiple-opening-closing-net with environmental sensing system (MOCNESS) tows was conducted aboard the RV *David Starr Jordan* (cruise DSJ-9203) during the 1992 spawning season. At that time, 21 tows were made in the area of

Pioneer and Ascension Canyons from 1800 h on 21 February to 0600 h on 23 February. Where bottom depth permitted, discrete depth samples were gathered using 505-µm mesh nets, sampling obliquely in the 0–40, 40–80, 80–120, 120–160, 160–200, 200–300, and 300–400 m depth intervals. Sampling was arrayed along seven onshore–offshore transects, each composed of three tows conducted at different bottom depths, i.e. mid-continental shelf (110 m), the shelf-break (183 m), and well off the shelf (550 m). All samples were preserved in EtOH and after sorting, identifying, and enumerating the larvae in the laboratory, we expressed abundances as the number of shortbelly rockfish larvae per 1000 m^3 water sampled.

Spawning seasonality

At its inception, this assessment was intended to be an application of the fecundity reduction method described by Lo et al. (1992, 1993). However, samples from the February and March adult trawl surveys showed that a higher proportion of females had completed spawning in the earlier cruise in comparison with the later cruise, an indication that sampling was not representative during one or both of the cruises. Consequently, the fecundity reduction method was abandoned and an alternative approach was devised. Instead, we estimated the seasonal distribution of spawning activity based on the temporal distribution of preflexion shortbelly rockfish larvae in samples collected as part of the CalCOFI program from December to April from 1952 to 1984 (see Ahlstrom et al., 1978). We then used this seasonal spawning pattern to expand our estimate of the daily spawning biomass from the short period represented by our 1991 plankton samples to the entire year.

To estimate the seasonal spawning distribution, we first identified the appropriate samples from CALCOFI station 63.55 in the vicinity of Pioneer Canyon by using results from MacGregor (1986) as a guide. Plankton samples at this location (Fig. 1) were re-examined and the total number of preflexion shortbelly rockfish larvae were enumerated from *Sebastes* subsets. These samples amounted to 41 plankton tows (bongo and ring nets) taken in 21 different years.

Next, we calculated the mean density of preflexion larvae for each month, assigned these densities to the midpoint day of the month, and used nonlinear least-squares regression to fit the normal curve to approximate the seasonal spawning pattern, i.e.

$$\hat{N}_p(t) = \frac{\Psi}{\hat{\sigma}_p\sqrt{2\pi}} e^{-\frac{(t-\hat{\mu}_p)^2}{2\hat{\sigma}^2}},$$

where $\hat{N}_{p(t)}$ = the estimated density of preflexion larvae on calendar day t (for December t is negative);

$\hat{\mu}_p$ = the expected value of the seasonal distribution of preflexion larvae;

$\hat{\sigma}_p$ = the standard deviation of the distribution; and

Ψ = a "nuisance" scaling constant.

To determine the seasonal distribution of age-0 larval production that generates the seasonal distribution of preflexion larvae, we assumed that the preflexion larval period has a duration of 15 days (Laidig et al., 1991) and that larvae experience the estimated preflexion mortality rate (see above). As with preflexion larvae, we approximated the seasonal distribution of age-0 larval production with a normal curve, with mean μ_0 and standard deviation σ_0. Given particular values for μ_0 and σ_0 we calculated the corresponding relative numbers of age-0 larvae produced during each day of the spawning season, and the integrated seasonal distribution of preflexion larvae, i.e.

$$N_p^*(t) = \sum_{i=0}^{15} N_0(t-i)e^{-iZ}$$

We started the estimation with trial values of μ_0 and σ_0 and then recursively adjusted the parameter estimates until the mean and standard deviation of the inferred seasonal distribution of preflexion larvae ($N^*_{p(t)}$) converged on the empirical estimates of $\hat{\mu}_p$ and $\hat{\sigma}_p$.

Lastly, based on the timing of the larval survey within the long-term mean spawning distribution, total biomass was calculated by simple expansion. Specifically, the midpoint of the 1991 bongo survey was 11 February (i.e. calendar day 42). Consequently we calculated λ, which is the proportion of annual spawning under the age-0 larval production curve that occurs from day 41.5 to 42.5. Total population biomass was then estimated by multiplying the estimate of "daily" biomass by $1/\lambda$. This calculation implicitly assumes that the seasonal progression of spawning has been stable over years. Therefore, the sensitivity of the biomass estimate to a violation of this assumption was evaluated by profiling over a range of values for the mean date of spawning (μ_0), which has a substantial effect on λ.

Precision of the biomass estimate

The determination of total biomass requires the estimation of numerous statistical relationships, each with its own parameter set. The results of fitting these functions were then combined algebraically to produce the final biomass estimate. We calculated the precision of the final biomass estimate by using the delta method (Seber, 1982, p. 8), i.e.

$$V\left[g(\theta)\right] = \sum_i V[\theta_i]\left(\frac{\partial B}{\partial \theta_i}\right)^2 + 2\sum_{i<j}\sum \operatorname{cov}\left[\theta_i,\theta_j\right]\frac{\partial B}{\partial \theta_i}\frac{\partial B}{\partial \theta_j},$$

where $g(\theta)$ = the algebraic combination of functions used to produce the final biomass estimates; and

θ = the full set of estimated parameters.

Application of this method requires estimates of variances for each parameter, covariances among parameters, and partial derivatives of estimated biomass with respect to each parameter ($\partial B/\partial\theta$). Partial derivatives of the final biomass estimate with respect to the parameters were calculated numerically by using central differencing by perturbing each parameter ±1% and calculating the resulting effect on biomass.

In some instances, variance estimates (i.e. squared standard errors) and covariances were extracted directly from computer output produced by the SAS (1987) procedures PROC REG and PROC NLIN. In the case of linear regressions, these are the usual estimates of these quantities (e.g. Draper and Smith, 1981), whereas for nonlinear regression, these are asymptotic variances and covariances (e.g. Seber and Wild, 1992). In addition, following the assumptions of normal-based regression, the residual error parameter estimates ($\hat{\sigma}^2_{mse}$) used in bias adjustments are independent of other regression parameters (i.e. covariances are zero) and $n\hat{\sigma}^2_{mse}/\sigma^2_{mse}$ has a chi-square distribution with k degrees of freedom, where k is the degrees of freedom associated with $\hat{\sigma}^2_{mse}$ (e.g. for a linear regression $k=n-2$). This chi-square distributed random variable, i.e.

$$\operatorname{var}\left(\frac{n\hat{\sigma}^2_{mse}}{\sigma^2_{mse}}\right) = 2k,$$

was then used to estimate the variance of the mean square errors (Larsen and Marx, 1981)

$$\operatorname{var}(\hat{\sigma}^2_{mse}) = \left(\frac{\hat{\sigma}^4_{mse}}{n^2}\right) \times 2k.$$

This straightforward approach to obtaining variances and covariances is appropriate when a suite of parameters estimated by a regression procedure is based on a data set that could reasonably be expected to be independent of data sets used to estimate other parameters, and when values of other estimated parameters were not used as "known" constants during a regression or estimation procedure. In two cases, however, estimates of other parameters were treated as known constants during a regression or estimation procedure. These cases were 1) estimation of the mean and standard deviation of the seasonal distribution of age-0 larvae, and 2) estimation of von Bertalanffy growth equation parameters. In the case of the seasonal distribution of age-0 larvae, parameter estimates depended upon the natural mortality rate estimated for larvae (Z). Hence, variances for these parameters calculated directly from the regression procedure are conditional on the estimated mortality rate. Imprecision associated with estimating this rate adds to variances of these parameters, and influences their covariance. Likewise, for von Bertalanffy growth, the weight "data" used were calculated on the basis of the estimated relationship between weight and length. Hence regression estimates of variance and covariances for the von Bertalanffy parameters are conditional on the parameters for the weight-length relationship. Uncertainty associated with the estimates of the weight-length parameters influences the unconditional variances and covariances of the von Bertalanffy parameters, sets up covariances between the two suites of parameters, and because the same weight-length relationship was used for both sexes, also sets up covariances among the von Bertalanffy parameters for males and females.

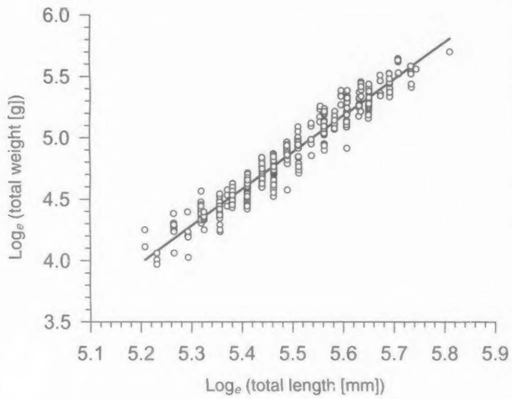

Figure 2

Fit of ordinary least-squares regression to log$_e$-transformed weight and length data from shortbelly rockfish sampled by trawl in February–March 1991.

For these cases, a generalized version of the delta method was used to estimate covariances (and variances):

$$\operatorname{cov}[g(x,y),h(x,z)] = \sum_{i}\sum_{j} \operatorname{cov}[x_i,x_j] \frac{\partial g}{\partial x_i}\frac{\partial h}{\partial x_j}$$

(Seber, 1982, p. 9). Here g and h represent regression procedures by which two specified parameters are estimated, x represents a set of shared values (assumed known parameters and data) used by the two regression procedures, y and z represent distinct data or parameters with no covariance among them, and partial derivatives are calculated as described above.

Results

Population weight-specific fecundity and sex ratio

The weight (W) of a fish is equated to its length (TL) by use of the power function, i.e.

$$W = \alpha TL^{\beta},$$

where α and β are fitted parameters (Ricker, 1975).

In our study, weight (gm) and TL (mm) data were collected from 352 fish sampled during the two adult trawl cruises. The data from these fish were log$_e$-transformed and fitted by linear regression (Fig. 2, Table 2). The fit was good, as indicated by a high r^2 value (0.94), and the distribution of residuals did not deviate from normality (P=0.109). To predict weight at length on the untransformed scale, a

Table 2

Functional relationships, estimated parameters, statistical results, and sensitivity analyses of shortbelly rockfish larval production biomass estimate.

Function	Parameter	Estimate	Standard error	% Effect on biomass	
				−1 SE	+1 SE
Length-weight relationship	$\log_e(\alpha)$	−11.512	0.2225	0.00%	0.00%
$\log_e(W) = \log_e(\alpha) + \beta(\log_e[TL])$	β	2.980	0.0405	0.09%	−0.08%
	σ^2_{MSE}	0.008820	0.000667	0.00%	0.00%
Female von Bertalanffy growth	$W_{\infty,\text{♀}}$,	248.1	2.6245	0.64%	−0.63%
$W_{\text{♀}} = W_{\infty,\text{♀}}\{1 - \exp[-K_{\text{♀}}(T - t_{0,\text{♀}})]\}^{\beta}$	$K_{\text{♀}}$	0.2843	0.00917	1.73%	−1.58%
	$t_{0,\text{♀}}$	−0.78	0.11026	−0.91%	0.96%
Male von Bertalanffy growth	$W_{\infty,\text{♂}}$,	209.9	3.0872	−0.67%	0.67%
$W_{\text{♂}} = W_{\infty,\text{♂}}\{1 - \exp[-K_{\text{♂}}(T - t_{0,\text{♂}})]\}^{\beta}$	$K_{\text{♂}}$	0.2432	0.00984	−2.05%	2.01%
	$t_{0,\text{♂}}$	−1.48	0.15183	1.55%	−1.54%
Adult survival	$\log_e(\eta_0)$	3.194	0.30662	0.00%	0.00%
$\log_e(N_T) = \log_e(\eta_0) - M(T)$	M	0.2616	0.02656	−1.46%	1.53%
Fecundity at weight	$\log_e(\phi)$	3.8155	0.1732	18.91%	−15.90%
$\log_e(F) = \log_e(\phi) + \delta(\log_e[W])$	δ	1.1416	0.0366	19.88%	−16.61%
	σ^2_{MSE}	0.2972	0.01827	0.92%	−0.91%
Maturity at length	v	2.888	0.0237	0.00%	0.00%
$S = 1 + v/\{1 + \exp[-\rho(TL - TL')]\}$	ρ	0.6046	0.10318	0.00%	0.00%
	TL'	135.05	0.85515	−0.15%	0.00%
Larval production and survival	$\log_e(N_0)$	−0.3775	0.1737	−15.97%	19.01%
$\log_e(N_T) = \log_e(N_0) - Z(T)$	Z	0.1107	0.01157	0.70%	−0.67%
	σ^2_{MSE}	0.1960	0.05659	−2.79%	2.87%
Spawning seasonality	Ψ	5.2×10^4	2.36×10^3	0.00%	0.00%
$N_p(t) = (\Psi/\sigma_p\sqrt{2\pi})\exp[-(t - \mu_p)^2/2\sigma_p^2]$	μ_p	37.88	1.1250	4.02%	−3.45%
	σ_p	17.39	1.1042	−4.58%	4.78%

bias-correction term ($\hat{\sigma}^2_{mse}/2$) was applied prior to exponentiation (Miller, 1984). However, because $\hat{\sigma}^2_{mse}$ was small (0.00882), the correction had little effect on predictions of weight at TL. Moreover, predicted values of weight at length did not differ materially from those given in Phillips (1964) and Lenarz (1980).

A total of 586 female shortbelly rockfish were aged from trawl samples. The weights (g) of these fish were individually estimated from measurements of TL (mm) by using the regression results described above. The derived weight-at-age (yr) data were then fitted to the von Bertalanffy growth equation by using a nonlinear regression routine (SAS, 1987). The specific form of the fitted model was

$$W_{\text{♀}} = W_{\infty,\text{♀}}\,[1 - e^{-K_{\text{♀}}(T - t_{0,\text{♀}})}]^{\beta},$$

where $W_{\text{♀}}$ = female weight (g)
$W_{\infty,\text{♀}}$ = the asymptotic mean weight of females at a hypothetically infinite age (g);
$K_{\text{♀}}$ = the instantaneous growth coefficient specific to females (/yr);
T = age (yr);
$t_{0,\text{♀}}$ = the x-intercept of the growth curve (yr); and
β = the allometric growth parameter estimated from the regression of weight on length (Ricker, 1975).

The β parameter is often set equal to 3.0, implying isometric growth, although β was fixed at 2.980 in this application (see above). Likewise, 535 adult male fish were aged, their weights estimated from measurements of TL, and the data fitted to the weight-based von Bertalanffy growth model. Regression results for both sexes are presented in Figure 3 and Table 2.

A simple exponential mortality model is used to describe the observed pattern of shortbelly rockfish abundance with age. The model is of the form

$$N_T = \eta_0 e^{-MT},$$

where N_T = the number of individuals alive at age T (yr);
η_0 = the extrapolated number at age T=0; and
M = the instantaneous rate of natural mortality (/yr).

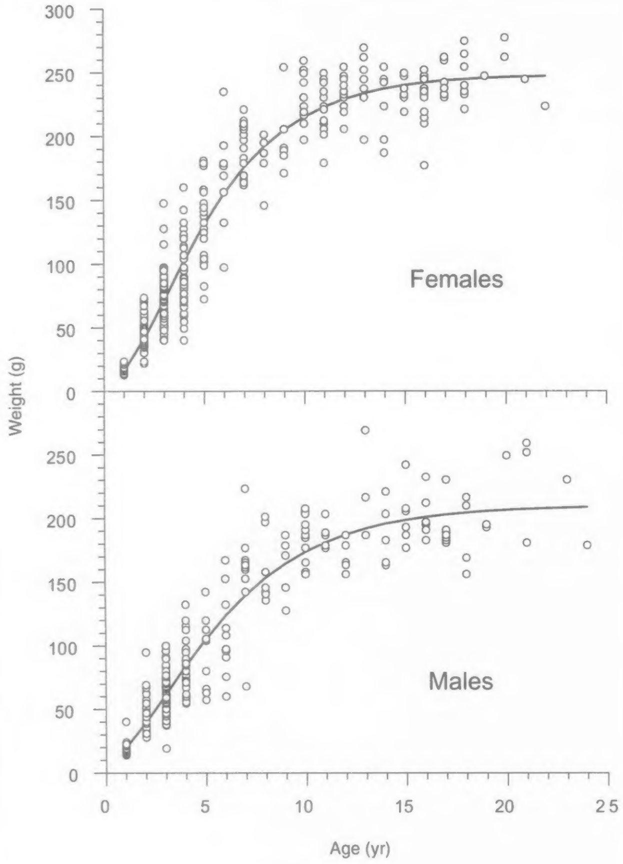

Figure 3

Weight-based von Bertalanffy growth curves fitted to shortbelly rockfish data collected by trawling during February–March 1991.

In this application a term for fishing mortality is assumed to be unnecessary because there is no commercial or recreational harvest of shortbelly rockfish. The model was fitted by a weighted linear regression of $\log_e(N_T)$ on T, where the statistical weights were derived from expansions of the aged subsamples to the full trawl catches. Results showed a declining trend in abundance with age (Table 2, Fig. 4), and an estimated adult natural mortality rate of 0.26/yr.

Like the weight-length relationship, fecundity is typically related to fish size with the power function (Bagenal and Braum, 1968), which is linearized by logarithmic transformation, i.e.

$$F = \phi W^{\delta},$$

$$\log_e(F) = \log_e(\phi) + \delta \times \log_e(W),$$

where F = individual annual fecundity (larvae/female);

W = female weight (g); and

$\log_e[\phi]$ and δ = fitted parameters.

In our study fecundity estimates were gathered from 531 females taken during the trawl surveys and the transformed data were fitted by simple regression (Fig. 5, Table 2). There was considerable residual variability in the fecundity at weight relationship (r^2=0.65; $\hat{\sigma}^2_{mse}$ =0.29715) and, in this instance, the addition of a bias-correction term had a noticeable effect on back-transformed predictions of fecundity at weight on the arithmetic scale. Although the distribution of regression residuals deviated significantly from normal (P=0.0001), due in large part to negative skewness, the overall fit was deemed adequate. Predictions of fecundity at weight were ~25–35% less than the results presented in Lenarz (1980), although his equation is based on only the 10 data points provided in Phillips (1964).

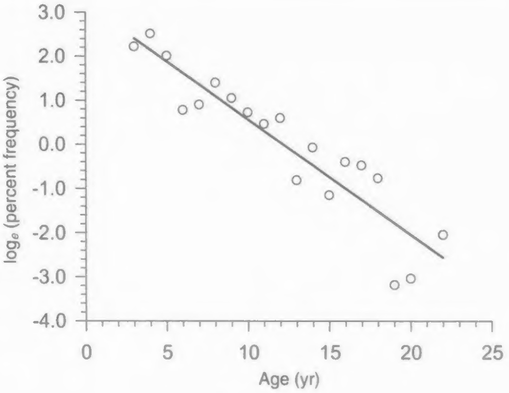

Figure 4

Weighted linear regression of log$_e$-transformed shortbelly rockfish abundance on age (statistical weights based on expansions of aged subsamples to full trawl catches; all samples collected by trawling during February–March 1991).

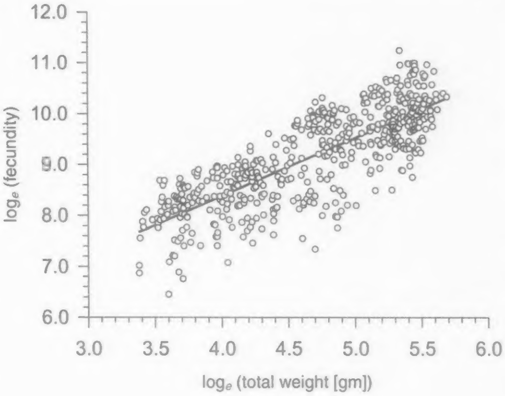

Figure 5

Fit of ordinary least-squares regression to log$_e$-transformed fecundity and weight data from shortbelly rockfish sampled by trawling during February–March 1991.

There was no evidence that the sex ratio of the fish sampled during the 1991 spawning season (n=1121 from February and March cruises combined) varied with age. A two-way test for independence of age and sex yielded χ^2=27.55, df=23, P=0.23. Moreover, there was no evidence that the overall population sex ratio was other than 50:50 ($N_{♀}$=586, $N_{♂}$=535; χ^2=2.32, df=1, P=0.14). From these results, we concluded that females and males both enter the population at approximately the same rate and thereafter they experience a similar natural mortality rate.

The maturity stage data were used to establish a maturity schedule for female shortbelly rockfish collected during the 1991 winter spawning season. Fish were first stratified by size class (5-mm-TL intervals), and for each size group, the mean coded ovarian stage was computed. The data were then fitted by nonlinear regression (SAS, 1987) to a logistic model of the form

$$S = 1 + \frac{v}{1+e^{-\rho(TL-TL')}},$$

where S = the mean coded maturity stage;
TL = total length (mm); and
v, ρ, and TL' = fitted parameters.

Results show (Fig. 6, Table 2) an abrupt change in ovarian condition at a length of 135 mm. At the time of sampling (February–March), virtually all fish above that size were gestating or had already released their larvae, whereas fish smaller than that cutoff size were almost exclusively immature. All females were therefore assumed to be reproductively mature if TL was greater than 135 mm. The proportion of fish in each age class that exceeded 135 mm TL was used to define an empirical age-based maturity ogive. Results indicated that 7.9% of 1-yr-old fish spawned, whereas 99.0% of 2-yr-old females reproduced.

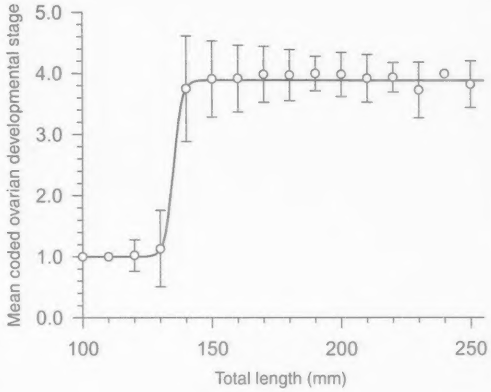

Figure 6

Fit of the logistic maturity function to coded ovarian developmental stage data. Circles are means, which are bracketed by ±1.0 standard deviation (all samples collected by trawling during February–March, 1991).

When coupled with some type of recruitment model, the four functional relationships given in Figures 3–6 can be used to estimate population weight-specific fecundity and a weight-based population sex ratio. These latter two variables are presented in Table 3 as part of a life table projection for shortbelly rockfish. In the table, age is incremented discretely in one year steps to a maximum life span of 30 yr, which extends well beyond the maximum observed age of 22 years (Pearson et al., 1991). All calculations were

Table 3

Life table for shortbelly rockfish (*Sebastes jordani*) based upon samples of adults obtained during the 1991 spawning season (February–March).

Age (yr)	♀ or ♂ numbers	♀ Wt (g)	♀ Cohort Wt (g)	Fecundity (larvae/♀)	Weight-specific fecundity (no. of larvae/g of female)	Proportion mature	Cohort fecundity (larvae)	♂ Wt (g)	♂ cohort Wt (g)
1	1.0000	15.9	15.85	1235	77.90	0.079	98	19.9	19.89
2	0.7698	41.0	31.54	3651	89.11	0.990	2783	39.6	30.50
3	0.5926	71.5	42.37	6893	96.42	1.000	4085	62.0	36.72
4	0.4562	102.4	46.72	10,390	101.45	1.000	4740	84.4	38.50
5	0.3512	130.8	45.93	13,736	105.03	1.000	4824	105.3	36.99
6	0.2704	155.3	41.98	16,710	107.61	1.000	4518	124.0	33.52
7	0.2081	175.6	36.55	19,227	109.50	1.000	4002	140.0	29.14
8	0.1602	192.0	30.76	21,291	110.89	1.000	3411	153.6	24.60
9	0.1233	205.0	25.28	22,943	111.93	1.000	2830	164.7	20.32
10	0.0950	215.1	20.43	24,245	112.70	1.000	2302	173.9	16.51
11	0.0731	223.0	16.30	25,258	113.27	1.000	1846	181.3	13.25
12	0.0563	229.0	12.89	26,040	113.70	1.000	1465	187.2	10.54
13	0.0433	233.6	10.12	26,640	114.02	1.000	1154	192.0	8.32
14	0.0333	237.2	7.91	27,098	114.26	1.000	904	195.8	6.53
15	0.0257	239.8	6.16	27,446	114.44	1.000	705	198.8	5.10
16	0.0198	241.8	4.78	27,710	114.58	1.000	548	201.1	3.98
17	0.0152	243.4	3.70	27,910	114.68	1.000	425	203.0	3.09
18	0.0117	244.5	2.86	28,061	114.76	1.000	329	204.5	2.39
19	0.0090	245.4	2.21	28,175	114.82	1.000	254	205.7	1.85
20	0.0069	246.1	1.71	28,261	114.86	1.000	196	206.6	1.43
21	0.0053	246.5	1.32	28,326	114.89	1.000	151	207.3	1.11
22	0.0041	246.9	1.02	28,375	114.92	1.000	117	207.9	0.85
23	0.0032	247.2	0.78	28,412	114.94	1.000	90	208.3	0.66
24	0.0024	247.4	0.60	28,440	114.95	1.000	69	208.7	0.51
25	0.0019	247.6	0.46	28,461	114.96	1.000	53	208.9	0.39
26	0.0014	247.7	0.36	28,476	114.97	1.000	41	209.1	0.30
27	0.0011	247.8	0.28	28,488	114.97	1.000	32	209.3	0.23
28	0.0009	247.8	0.21	28,497	114.98	1.000	24	209.4	0.18
29	0.0007	247.9	0.16	28,504	114.98	1.000	19	209.6	0.14
30	0.0005	247.9	0.13	28,509	114.98	1.000	14	209.6	0.11
Total		411.37					42,028		347.65

based on a discrete time origin that was centered in the spawning season and it was assumed that samples were obtained at that time.

For simplicity, constant annual recruitment to the population at age 1 is assumed, although this particular assumption is later relaxed and its specific effect on estimates of population weight-specific fecundity is evaluated. To start the simulated population, recruitment was arbitrarily set equal to N_1 = 1.0/yr for both females and males. Then, given female weight at age (Fig. 3) and female numbers at age (Fig. 4), one can calculate age-specific female cohort biomass as the product of numbers and individual weights (Table 3), which when summed over all ages yields the total equilibrium female biomass (411.37 g/female recruit). Likewise, age-specific cohort fecundity is calculated as female numbers at age, multiplied by estimates of individual female fecundity (Fig. 5), multiplied by the proportion of females that are mature (Fig. 6), which when summed over all ages classes yields the expected lifetime larval production of a cohort (42,028 larvae). The ratio of these two quantities (Φ=102.17 larvae/g of female) estimates the population weight-specific fecundity of female shortbelly rockfish. This population statistic can be compared with individual age-specific estimates presented in Table 3. These weight-specific fecundities range from 77.90 larvae/g of female for the mature 1-yr-old females, to 114.98 larvae/g of female for the oldest fish.

It is also revealing to compare predicted weight-specific fecundity at age from the life table analysis (Table 3) with the observed data calculated directly from individual fish (Fig. 7). Results show a great deal of variability in the observed data, which is consistent with the extensive residual variability in fecundity (see Fig. 5, Table 2). Life table predictions were generally similar to, but slightly higher than, the observed data. This slight difference is

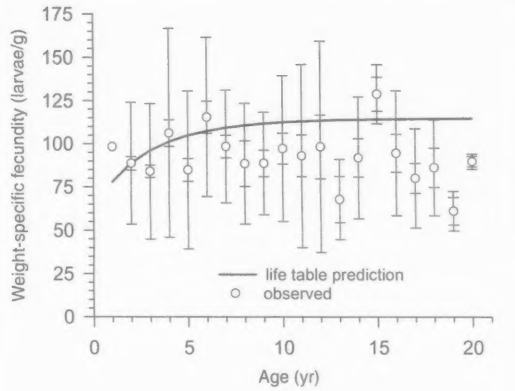

Figure 7

Weight-specific fecundity and its dependency on age. Observed values are means of measured females, bracketed by ±1.0 standard error and ±1.0 standard deviation (all samples collected by trawl during February–March, 1991). The solid line, which is not fitted to the "observed" points, is the predicted relationship from the life table analysis presented in Table 3.

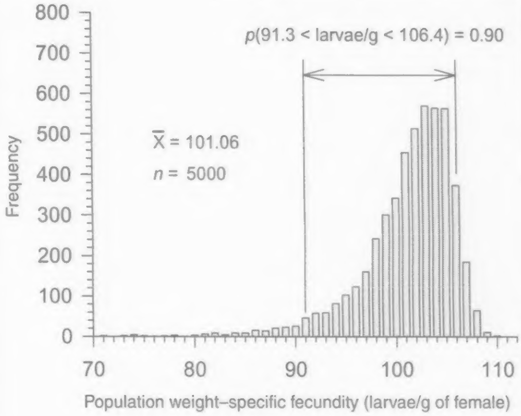

Figure 8

Results of Monte Carlo simulation evaluating the effect of recruitment stochasticity on calculations of shortbelly rockfish population weight-specific fecundity.

due to the bias correction that occurs when the fecundity relationship, which was fitted on the log-scale, is back-transformed to the arithmetic scale. Irrespective of the type of data, however, it is evident that weight-specific fecundity is only weakly dependent on age. This finding implies that changing the equilibrium age structure of the population, as mediated through an alteration in the natural mortality rate (M), will have little effect on the population's weight-specific fecundity.

The assumption that recruitment is constant and uniform does not appear to appreciably bias the estimate of population weight-specific fecundity derived from the life table analysis (102.17 larvae/g of female). Population weight-specific fecundity was also estimated in a Monte Carlo life table simulation that used a more realistic lognormal recruitment model (Fogarty, 1993). Annual recruitments in that simulation were determined as $N_1 = \exp(\mu + \sigma X)$, where N_1 is the number of recruits at age 1, $\mu = \log_e[10{,}000]$, $\sigma = 0.921$, and X is a standard normal deviate (i.e. $X \sim N[0,1]$). This level of variability in lognormal recruitment is comparable to that observed in the widow rockfish fishery (Bence et al., 1993; Hightower and Lenarz[3]), where 20-fold differences in recruitment have been observed in a 10-yr time period. Results of the simulation showed that fluctuating, lognormal recruitment can produce values of population weight-specific fecundity that range from 71 to 110 larvae/g of female, depending on the exact sequence of year classes and their resulting affect on age structure (Fig. 8). Even so, the mean of the sample distribution ($\bar{x}$=101.06 larvae/g of female, n=5000) did not differ significantly from the life table calculation that had no recruitment variability. In addition, 90% of all the lognormal recruitment realizations were within ±10% of the constant recruitment result.

By definition, population weight-specific fecundity represents the number of larvae produced by one gram of female biomass (including immature 1-yr-olds). We expanded female biomass to total biomass including males. Results presented in Table 3 show that age-specific male cohort biomass, like that of females, is calculated as the product of numbers-at-age and individual weights-at-age, which when summed over all ages yields the total equilibrium male biomass (347.64 g/male recruit). Total population biomass (i.e. females+males) is then 759.01 g, of which females comprise 54.2% by weight. Thus, the total biomass is estimated by applying a 1.845 expansion factor to female biomass.

Larval production

Sampling with different mesh-size bongo nets (333 and 505 µm) allowed an assessment of whether a portion of smaller larvae retained by the smaller mesh was lost with the standard 505-µm mesh. Although shortbelly rockfish are relatively large and stout at parturition (~5.0 mm, Moser et al., 1977), undersampling of small, young larvae could seriously bias larval production estimates. Results presented in Figure 9 show, however, that the standardized catches of larvae (number/[10 m^2]) in the two net sizes were quite similar. A paired t-test of catches (333 minus

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[3] Hightower, J. E., and W. H. Lenarz. 1990. Status of the widow rockfish fishery in 1990. *In* Status of the Pacific coast groundfish fishery through 1990 and recommended acceptable biological catches for 1991. Stock assessment and fishery evaluation, appendix vol. 2, 48 p. Pacific Fishery Management Council, Portland, OR.

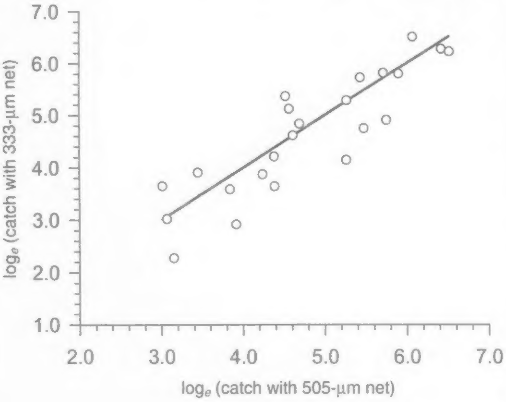

Figure 9

Paired comparison of $\log_e$-transformed larval shortbelly rockfish catches taken in bongo nets with different mesh sizes (all samples collected during February 1991). Also shown is the line of equality.

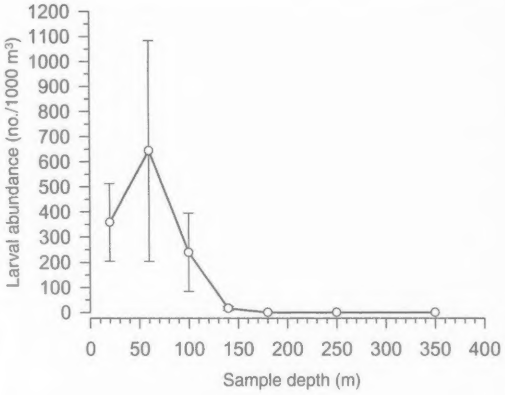

Figure 10

Mean catch rate of shortbelly rockfish larvae in seven depth strata taken by a MOCNESS sampler during March 1992. Means are bracketed by ±1.0 standard error.

505) resulted in $\bar{x} = -0.1458$, $n = 23$, $t = -1.24$, and $P = 0.23$, indicating no difference in the catch of the larger mesh net in relation to the smaller net. We conclude that the 505-µm net was an effective sampler of rockfish larvae.

Examination of the standardized catches from the MOCNESS tows conducted in 1992 revealed that shortbelly rockfish larvae were not caught in depths below the 120–160 m interval (Fig. 10). The mean catch rate in that depth range was 16.8 larvae/1000 m^3, which amounted to only 1.3% of the combined average catch at all depths, i.e. 98.7% of all larvae were captured at depths < 120 m. Because the bongo net was deployed to a maximum depth of 140 m in 1991, and because the mixed layer depth was depressed during MOCNESS sampling in 1992 due to strong El Niño conditions (Lynn et al., 1995), we concluded that the 1991 bongo net survey sampled the entire depth range where shortbelly rockfish larvae occurred.

For this assessment, a total of 2203 shortbelly rockfish larvae were subsampled from the 505-µm bongo net catches and were aged by using optical microscopy (see Ralston et al., 1996). Results from that work indicated that the ages were quite precise (84% agreement among three readers to within ±1 d) and there were, moreover, no increment interpretation differences between optical observations and those made with a scanning electron microscope (SEM).

The horizontal distribution of very young (0–2 d) shortbelly rockfish larvae was strongly associated with the continental shelf break (Fig. 11) and, latitudinally, with the Pioneer Canyon area. Due to the coincidence of this distribution with the locus of adult sampling sites (Fig. 1), we concluded that the trawl survey sampled the adults that produced the larvae captured in the ichthyoplankton survey. This finding supports the coupling of our population weight-specific fecundity statistic (102.17 larvae/g of female) with larval production to estimate the total biomass of shortbelly rockfish in the Pioneer Canyon region. Although not shown, older age classes of larvae tended to be more dispersed and to occur increasingly to the northwest—a pattern consistent with hydrographic conditions at the time of the survey (Sakuma et al., 1995).

When Sette-Ahlstrom weights were used to expand age-specific standardized bongo net catches to the entire study region, the composite age-frequency distribution of shortbelly rockfish larvae appeared to support a $\log_e$-linear model with constant exponential mortality (Z [/d]), i.e.

$$N_T = N_0 e^{-ZT}, \log_e(N_T) = \log_e(N_0) - ZT,$$

where N_T = the total abundance of larvae of age T (d);
Z = the instantaneous larval mortality rate (/d); and
N_0 = the larval renewal rate (i.e. daily production of larvae).

The model was fitted over the first 25 days of life, which largely represents the preflexion stage. In addition, the N_T were first coded by scaling all observations to 1×10^{11} and 0.5 was added to all larval ages as a continuity correction (see Ralston et al., 1996). Results show (Fig. 12, Table 2) a satisfactory fit, although there is some suggestion of an aberrant, serially correlated pattern in the residuals from age 0–9 d. The *y-intercept* term ($\log_e[N_0] = -0.3775$), when back-transformed (with bias-correction) yields $\hat{N}_0 = 7.562 \times 10^{10}$ age-0 larvae.

Given estimates of daily larval production (7.562×10^{10} larvae) and population weight-specific fecundity (Φ= 102.17 larvae/g of female), we calculated from the ratio of these two quantities that 740 t of female shortbelly rockfish spawned each day during the bongo net cruise (DSJ-9102), which is equivalent to a daily biomass of 1366 t/d (sexes combined).

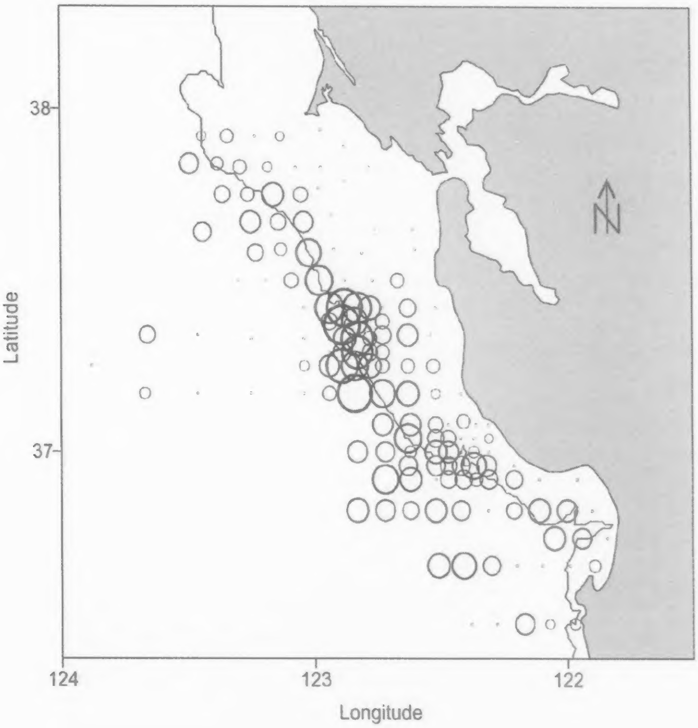

Figure 11

Map showing the spatial distribution of very young (0–2 d) shortbelly rockfish larvae sampled during February 1991. The size of the circles is proportional to $\log_e$(catch+1).

Historical data from CalCOFI station 63.55 (Fig. 1) showed that in the vicinity of Pioneer Canyon the seasonal availability of preflexion shortbelly rockfish larvae peaks during January–March (see "observed" in Fig. 13). These data were fitted to a normal curve (see "predicted" in Fig. 13) and indicated that the distribution of preflexion larvae is centered on 7 February (calendar date $\hat{\mu}_p$= 37.88) and the spawning season typically lasts ~70 d ($\hat{\sigma}_p$=17.39). Assuming that preflexion larvae represent a pool of fish 1–15 d old (Laidig et al., 1991) that experience a daily instantaneous mortality rate of $Z = 0.11$/d (Table 2), the distribution of age-0 larval production is centered earlier in the spawning season, i.e. 2 February (calendar date $\hat{\mu}_0$ =32.62) and the spawning season is slightly less protracted ($\hat{\sigma}_0$=16.86). The estimated long-term mean distribution of age-0 larval shortbelly rockfish production at CalCOFI station 63.55 (Fig. 1) is depicted in Figure 13 as a solid line.

The midpoint of the 1991 bongo-net survey (DSJ-9102) was 11 February (calendar date 42). If larval production were normally distributed and centered at $\hat{\mu}_0$ = 32.62, with $\hat{\sigma}_0$ = 16.86, we calculated that the area under the curve from 41.5 to 42.5 is 0.02026. This represents the estimated fraction of the total annual larval production that occurred per day at the midpoint of the cruise and is the area under the curve between the two vertical lines shown in Figure 13. Thus, we expanded by 49.35 spawning d/yr (1/0.02026) the estimated daily biomass (1366 t/d) to 67,392 t/yr, which is the estimated total stock biomass of shortbelly rockfish in the study area. The standard error of this estimate, based upon delta-method computations, is 12,900 t/yr, yielding a coefficient of variation of 19%.

Sensitivity of the biomass estimate

Presented in Table 2 is a simple sensitivity analysis of all parameters estimated in the larval production spawning stock biomass assessment of shortbelly rockfish. For each of the 23 parameters, the coefficient of variation (expressed as a percentage) is given. In addition, the effects of individual parameter perturbations on the final estimate of spawning stock biomass are shown. In each case, a parameter (Θ) was altered by plus or minus one standard error of the estimate (s_Θ) and the resulting overall effect on the assessment was expressed as the percentage change of the perturbed biomass estimate in relation to the unperturbed value, i.e.

$$\Delta_e = 100\left[\frac{B_\theta - B_0}{B_0}\right],$$

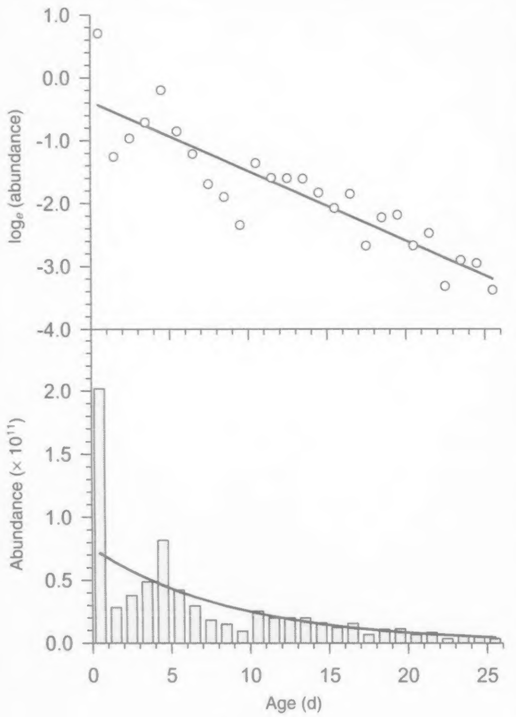

Figure 12

Fit of ordinary least-squares regression of log$_e$-transformed coded larval abundance ($\hat{n}\times10^{-11}$) on corrected larval age (T+0.5) (upper panel). The lower panel shows the back-transformation of the log$_e$-linear model (with bias correction) superimposed on the original abundance data.

where Δ_Θ = the relative sensitivity of the assessment to parameter "Θ";

B_Θ = the resulting biomass after altering parameter "Θ" by $\pm s_\Theta$; and

B_0 = the original unperturbed biomass estimate (67,392 t/yr).

Perturbations equal to $\pm 1\ s_\Theta$ were selected to reflect the level of statistical uncertainty in the parameters themselves. Results showed that within this range of uncertainty, certain parameters had essentially no effect on the final estimate of spawning stock biomass (e.g. log$_e$[η_0], ν, ρ, Ψ), and others had a more substantial effect. In particular, the assessment was most sensitive to estimates of the two fecundity parameters (log$_e$[ϕ] and δ) and to the intercept term of the larval production and survival model (log$_e$[N_0]); both of these findings are consistent with intuition.

Also note that the estimate of adult natural mortality rate (M) has only a minor influence on projected biomass. Low sensitvity to this parameter is important because M alone governs the adult age-structure, implying that variation in age-structure has little effect on the overall stock assessment. This conclusion was portended by results presented in Figures 7 and 8, which illustrate the relative insensitivity of weight-specific fecundity to age. Fundamentally, this conclusion is due to the nearly linear relationship between individual female fecundity and specimen weight (δ=1.14, Table 2, Fig. 5); that is, a fixed mass of mature females produces roughly the same larval output, irrespective of its age composition.

This property is quite useful because it suggests that an accurate estimate of M is not required to make useful projections of total biomass. As discussed previously, obtaining a representative sample of adult rockfish is difficult (Lenarz and Adams, 1980); yet such a sample is usually needed to estimate mortality. Pearson et al. (1991) also highlighted the problem of estimating the natural mortality rate of shortbelly rockfish. Using empirical longevity estimates ($T_{max,♀}$=22 yr, $T_{max,♂}$=20 yr) as inputs to Hoenig's (1983) regression equation and sample size model, they concluded that for shortbelly rockfish $0.20 \le M \le 0.35$/yr. Even over this rather broad range of plausible natural mortality values, our results indicate that biomass estimates vary by only ~9% (Fig. 14).

In contrast, mis-specification of the temporal progression of spawning could have a very large effect on the total biomass estimate. Results presented in Figure 15 show the sensitivity of the total biomass estimate to a range of values for μ_0. Because this parameter depends directly on μ_p and σ_p, which were estimated with good precision (Table 2), the expected effect on the total biomass estimate is relatively minor. Even so, if the mean of the spawning distribution actually occurred two weeks earlier (i.e. 18 January instead of 2 February), the biomass estimate would be grossly in error.

Discussion

It is widely recognized that most age-structured stock assessments depend critically on the availability of auxiliary information to adequately constrain solutions to these complex models (Deriso et al., 1985; Hilborn and Walters, 1992; NRC 1998; Quinn and Deriso, 1999). However, even with lengthy time series of landings, discards, age compositions, length compositions, survey CPUE data, and logbook effort statistics, it is by no means certain that complex stock assessment models will precisely or accurately estimate total stock biomass (NRC, 1998). Faced with this dilemma, simple procedures like the one presented here become far more attractive, particularly because the coefficient of variation on the final biomass estimate from this pilot study was relatively precise (i.e. 19%). Moreover, the estimate of absolute biomass does not depend on the development of a long time series of data and it can be obtained rather quickly.

We note that in comparison with previous hydroacoustic assessments, which ranged from 153,000–295,000 t,[1] our estimate of the total biomass of shortbelly rockfish in the vicinity of Pioneer and Ascension Canyons (67,400 t) is substantially lower. Because one of the primary goals of our study was to obtain a more precise biomass estimate than the hydroacoustic estimates, it is important to care-

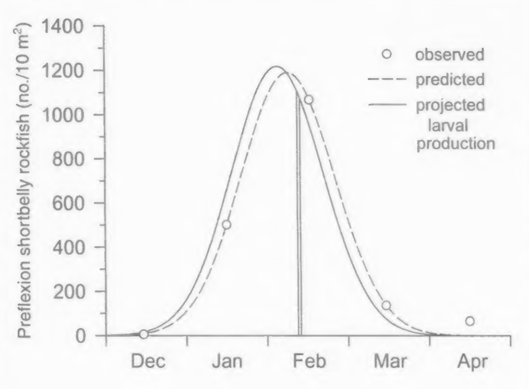

Figure 13

Seasonal pattern in the catch of preflexion shortbelly rockfish larvae at CalCOFI station 63.55 (Pioneer Canyon; see Fig. 1). Observed data were fitted with a normal curve; projected larval production assumes M = 0.11/d.

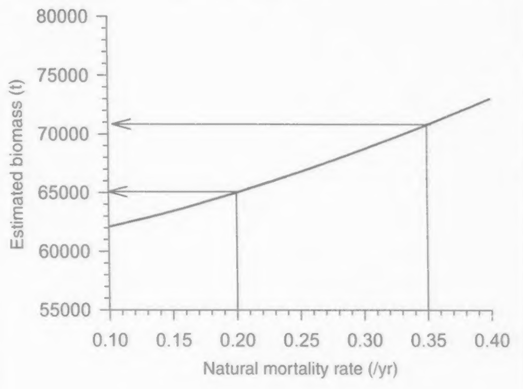

Figure 14

Sensitivity of the larval production estimate of shortbelly rockfish total biomass to the estimated natural morality rate. Vertical dashed lines extending up from the abscissa encompass the likely range of shortbelly rockfish natural mortality (Pearson et al., 1991).

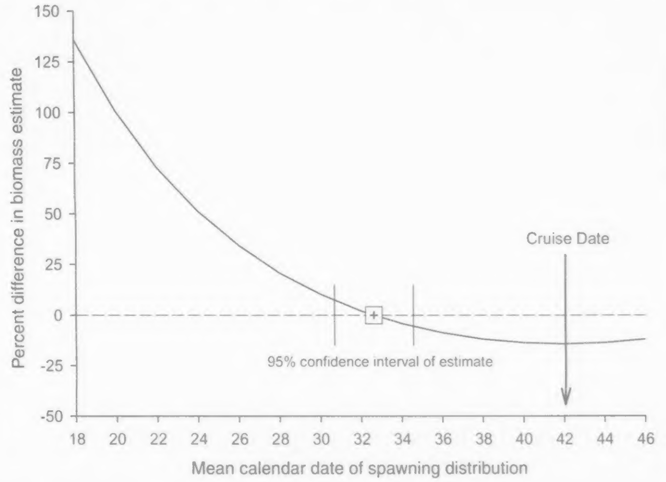

Figure 15

Sensitivity of the total biomass estimate to the mean of the seasonal distribution of shortbelly rockfish larval production, based on CalCOFI samples collected at station 63.55. The estimated mean (μ_0=32.62) is represented by the square, which is bounded by its 95% confidence interval. The effect of misspecifying μ_0 over a broader range (i.e. ±2 weeks) is also shown.

fully consider sources of error and uncertainty in the larval production estimate.

Results presented in Table 2 show that errors in estimating the six growth curve parameters had negligible effects on the biomass estimate, ranging at most from –2.05% to +2.01%. However, estimation errors in the logarithmically transformed power function regression of fecundity on weight had a considerably greater effect. Parameter perturbations in this function altered biomass estimates by ~15–20%. In contrast, errors in estimating the parameters of the logistic maturity ogive had virtually no effect.

We have shown that weight-specific fecundity was only weakly dependent on age (Fig. 7). If these variables were independent, the age structure of the stock would have no influence on population fecundity; that is, a ton of 5-yr-old fish would have the same reproductive output as a ton of 20-yr-old fish. Thus, if age and weight-specific fecundity are independent, the natural mortality rate (M) has no influence on the estimation of biomass, which agrees with the relative insensitivity of the total biomass estimate to estimated natural mortality rate (Table 2, Fig. 14). This a highly desirable characteristic of the assessment methods proposed here. Unlike stock assessments that are predicated on measuring the abundance of ichthyoplankton, results from standard age-structured stock assessment models often depend critically on what is almost always an assumed value of M (e.g. Ralston and Pearson[4]). This can have the effect of reducing an entire stock assessment modeling exercise to guesswork.

Daily larval production ($\log_e[N_0]$) is the other estimated parameter that most strongly influences the calculation of biomass, with parameter perturbations of ±1.0 standard error that result in a 16–19% effect on estimated stock biomass (Table 2). This parameter was determined by assuming a constant mortality rate model, which yielded $Z = 0.11/\text{d}$. However, we view the selection of a specific mortality model to be of considerable importance and wish to emphasize that other alternatives to the exponential survivorship case are available, including the Pareto model (Lo et al., 1989). Researchers who wish to apply the method that we outline here would be well-advised to examine this particular issue carefully because the estimate of daily larval production (N_0) will depend critically on the mortality model used.

Another underlying assumption of the larval production method is that over the period represented by the data, the larval production rate and the mortality rate remained constant. Violations of this assumption could cause patterns like those evidenced in Figure 12. However, we conclude that the existing data do not allow us to distinguish between explanations based on correlated estimation errors and those based on time-varying larval production rates. Also, the ichthyoplankton survey took place over a 6½-day period and samples close together in space were also close together in time, which further complicates the issue. Possible future approaches might consist of sampling designs that include spatial and temporal replication.

Another major source of uncertainty in our assessment lies in the expansion of "daily" total biomass to "annual" total biomass. Based upon the long-term mean distribution of spawning activity (Fig. 12), we calculated that the annual biomass was ~50 times larger than the daily biomass on 11 February. Use of the long-term mean distribution has obvious limitations, however, if the spawning season varies interannually (see Fig. 15).

Results presented in MacGregor (1986) can be used to examine the assumption that spawning seasonality is the same every year. He sorted all shortbelly rockfish larvae from all plankton samples that were collected as part of CalCOFI surveys conducted in 1956, 1966, 1969, 1972, and 1975. In each of these years, cruises were conducted in every month and he presented monthly total larval abundances by year in tabular form. His findings showed that, within the region bounded by CalCOFI lines 60–137 (i.e. San Francisco, CA, to Magdalena Bay, Mexico), the mean date of preflexion larval abundance (μ_p) encompassed only four days among those five years, which together spanned two decades. Similarly, with the exception of 1972 (an El Niño year) the standard deviation of the preflexion larval distribution (σ_p) varied by only five days. These results are consistent with other studies that have shown a remarkable consistency in the timing of fish reproduction (Cushing, 1969; Anderson, 1984; Pedersen, 1984; Picquelle and Megrey, 1993; Gillet et al., 1995; but see Hutchings and Myers, 1994). Thus, although misspecification of the mean time of spawning has the potential to seriously impact the biomass estimate, the observed data suggest that in this application the effect is negligible.

Perhaps a more important structural assumption we have made is that the spawning season can be represented by a normal distribution. Although Saville (1956, 1964) advocated use of the normal distribution for this purpose, we question the generality and accuracy of this symmetric function when used to model spawning seasonality. In the case of shortbelly rockfish, the fit of the five data points to the distribution was reasonably good (dashed line in Fig. 13). Even so, we note that the observed data were monthly means and the April value did not conform well to expectation. Therefore, in future applications of the larval production method we recommend strongly that a well-defined year-specific estimate of the seasonal distribution of spawning activity (i.e. the production rate of age-0 larvae) be obtained. In principle these data could be gathered by high-frequency sampling of either the larval or adult portions of the stock, and even through monitoring the maturity of females in commercial landings.

It is also true that the entire spatial distribution of early larvae must be surveyed in order for the larval production estimate ($\hat{N}_0$) to represent the complete spawning stock. This concern is not unique to this assessment, however; it is a requirement that must be satisfied whenever egg and larval surveys are used to estimate the absolute biomass of a fish stock. Nonetheless, in this application it is not likely to have been fully met (Fig. 11). Although the primary spawning concentration of shortbelly rockfish along the central California seems to have been largely encompassed, there is evidence that the offshore extent of very young larvae was not fully captured

Acknowledgments

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[4] Ralston, S., and D. Pearson. 1997. Status of the widow rockfish stock in 1997. *In* Status of the Pacific coast groundfish fishery through 1997 and recommended acceptable biological catches for 1998. Stock assessment and fishery evaluation, appendix, 54 p. Pacific Fishery Management Council, Portland, OR.

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Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require?

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Abstract—The effects of seasonal and regional differences in diet composition on the food requirements of Steller sea lions (*Eumetopias jubatus*) were estimated by using a bioenergetic model. The model considered differences in the energy density of the prey, and differences in digestive efficiency and the heat increment of feeding of different diets. The model predicted that Steller sea lions in southeast Alaska required 45–60% more food per day in early spring (March) than after the breeding season in late summer (August) because of seasonal changes in the energy density of the diets (along with seasonal changes in energy requirements). The southeast Alaska population, at 23,000 (±1660 SD) animals (all ages), consumed an estimated 140,000 (±27,800) t of prey in 1998. In contrast, we estimated that the 51,000 (±3680) animals making up the western Alaska population in the Gulf of Alaska and Aleutian Islands consumed just over twice this amount (303,000 [±57,500] t). In terms of biomass removed in 1998 from Alaskan waters, we estimated that Steller sea lions accounted for about 5% of the natural mortality of gadids (pollock and cod) and up to 75% of the natural mortality of hexagrammids (adult Atka mackerel). These two groups of species were consumed in higher amounts than any other. The predicted average daily food requirement per individual ranged from 16 (±2.8) to 20 (±3.6) kg (all ages combined). Per capita food requirements differed by as much as 24% between regions of Alaska depending on the relative amounts of low–energy-density prey (e.g. gadids) versus high–energy-density prey (e.g. forage fish and salmon) consumed. Estimated requirements were highest in regions where Steller sea lions consumed higher proportions of low–energy-density prey and experienced the highest rates of population decline.

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Nutritional stress may account for the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska (Alverson, 1992), which have declined by over 70% in the last 20–25 years (Loughlin et al., 1992; Trites and Larkin, 1996). Merrick et al. (1997) found a negative correlation between Steller sea lion diet diversity and the rate of population change among six regions of Alaska in the early 1990s. The greatest rates of population decline occurred in areas with low diet diversity, where Steller sea lions predominantly preyed on either walleye pollock or Atka mackerel. Steller sea lions from areas that did not experience a decline, or experienced a lower rate of decline, preyed on both walleye pollock and Atka mackerel along with several other groups of prey species.

Merrick et al. (1997) suggested that the relationship between diet diversity and the rate of population decline reflected differences in the efficiency with which Steller sea lions could find, capture, and handle different numbers of prey categories. However, the energy content of the diet may also have a substantial effect on the foraging efficiency of Steller sea lions. Steller sea lions consuming a low diversity diet of primarily low–energy-density species (e.g. gadids) need to consume more prey biomass than Steller sea lions eating a more diverse diet including high–energy-density species (e.g. forage fish, salmon) to obtain the same amount of energy. Thus, it may be more difficult for Steller sea lions consuming a diet of low-energy content to meet their energy requirements or to forage efficiently than it would be for animals consuming prey of high-energy content.

The overall goal of our study was to estimate the amount of prey required by Steller sea lions in Alaska during the 1990s using a previously developed bioenergetic model (Winship et al., 2002). Our first objective was to examine how daily food biomass requirements were affected by seasonal differences in the energy density of the diet of Steller sea lions in southeast Alaska. Our second objective was to use the same model to compare the food requirements of Steller sea lions among seven regions of Alaska during the 1990s (regions based on Merrick et al., 1997, and Sease and Loughlin, 1999; Fig. 1). Our third objective was to use data from 1998 to compare estimates of Steller sea lion prey consumption with fisheries catches and estimates of prey stock sizes (and natural mortality rates).

Methods

Model structure

The bioenergetic model that we used is described in detail by Winship et al. (2002). In brief, gross energy requirements were calculated for individuals of each age, sex, reproductive status (immature, mature, pregnant), and day of the year by using information on Steller sea lion energetics (basal metabolic rates, active metabolic rates, activity budgets, body growth and composition, digestive efficiency and the

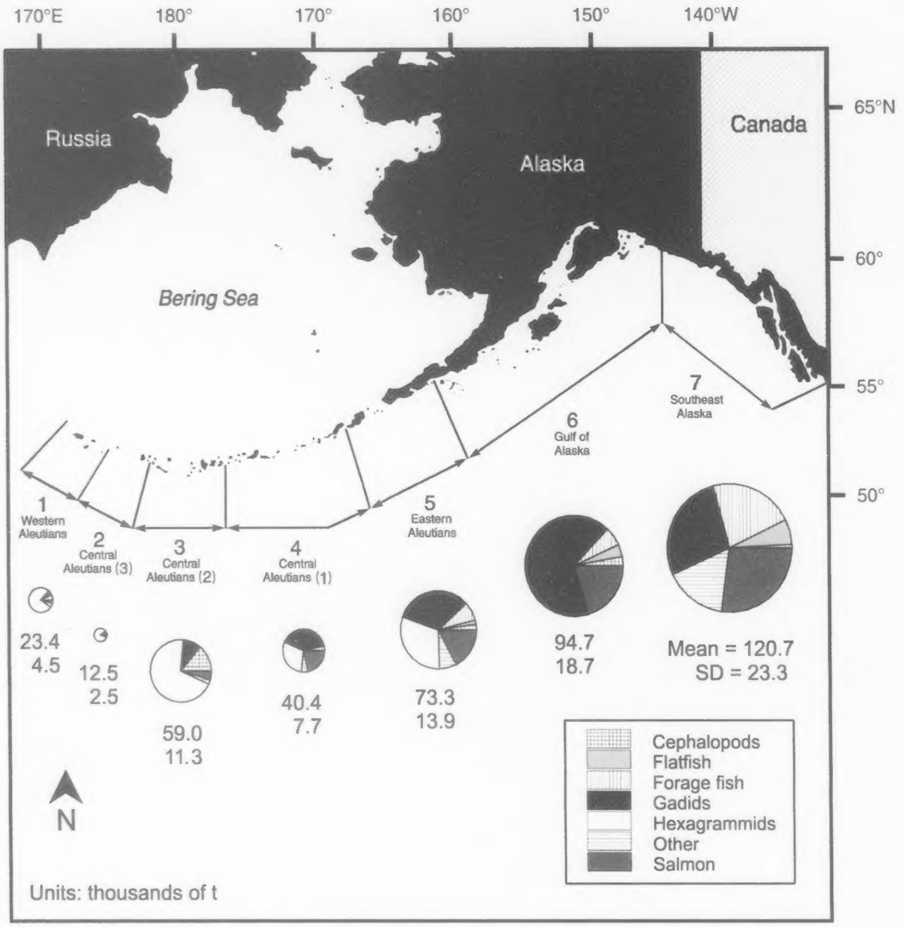
170°E
180°
170°
160°
150°
140°W
65°N
60°
55°
50°
Russia
Canada
Alaska
Bering Sea
1 Western Aleutians
2 Central Aleutians (3)
3 Central Aleutians (2)
4 Central Aleutians (1)
5 Eastern Aleutians
6 Gulf of Alaska
7 Southeast Alaska
23.4
4.5
12.5
2.5
59.0
11.3
40.4
7.7
73.3
13.9
94.7
18.7
Mean = 120.7
SD = 23.3
Cephalopods
Flatfish
Forage fish
Gadids
Hexagrammids
Other
Salmon
N
Units: thousands of t

Figure 1

Estimated annual food biomass requirements (thousands of t) for Steller sea lions in 1998 in seven study areas of Alaska assuming that the summer diets were consumed all year long. SDs were obtained by using Monte Carlo simulations (1000 runs). Pie charts represent the proportions of diet biomass that each prey species category represents (defined in text). Diameters of the pie charts are proportional to their respective mean food requirement estimates. The map and study areas were adapted from Merrick et al. (1997) and Sease and Loughlin (1999). Numbers in parentheses in the central Aleutians (areas 2–4) are subarea numbers.

heat increment of feeding or the efficiency of using metabolizable energy). Metabolizable energy requirements of individuals were assumed to be the same in all regions of Alaska. Gross energy requirements of individuals were expected to vary among regions of Alaska because digestive efficiency and the heat increment of feeding are dependent upon the energy density of the diet, which varied among regions. Next, population size and composition were calculated by using pup count data from 1998, and a life table for Steller sea lions in Alaska. Population size varied by region of Alaska, but we assumed that population composition (i.e. sex and age structure) was the same for all regions. Finally, food requirements were calculated by assuming a given diet composition (percent contribution of each prey category to diet biomass) and by using information on the energy density of prey. Diet composition varied by region of Alaska, but we assumed the energy density of individual prey categories did not.

The model incorporated a Monte Carlo random sampling routine which allowed us to estimate the error in the model predictions based on the assumed uncertainty in each parameter value. Three types of parameter sampling distributions were used: uniform (defined by upper and lower limits; e.g. 0.1–0.3), triangular (defined by a median, an upper limit and a lower limit; e.g. 0.2, 0.1–0.3), and normal (defined by a mean and SD; e.g. 0.2 ±0.05).

It is important to note that the model estimates of daily food requirements are not estimates of daily food consumption (Winship et al., 2002). Steller sea lions do not necessarily feed on a daily basis and breeding adults fast for periods during the breeding season. For example, the food required by a breeding male during the breeding season fast (to meet its energy requirement) would have been consumed before or after the breeding season (i.e. outside the breeding season). On an annual basis, however, the model estimates of food requirements are equal to food consumption if animals are consuming enough food to meet their energy requirements. We assumed that the amount of food consumed by the Steller sea lion population in Alaska in 1998 equaled the food requirement of the population.

Bioenergetic parameters

We used sampling distributions for bioenergetic parameters that were identical to those used by Winship et al. (2002) with the exception of fecal digestive efficiency and the heat increment of feeding for maintenance (for nonpups). Winship et al. (2002) defined fecal digestive efficiency as 1 minus the proportion of gross energy lost in feces, and assumed that its value ranged from 0.90–0.96 for Steller sea lions (i.e. fecal digestive efficiency was sampled from a uniform distribution). However, several studies have shown that the digestive efficiency of pinnipeds is positively correlated with the energy density of their prey (Keiver et al., 1984; Mårtensson et al., 1994; Lawson et al., 1997). In contrast, two other studies found that the digestive efficiencies of pinnipeds did not differ significantly among diets of different energy densities, although in both studies the average digestive efficiency was highest for the diet with the highest energy density (Fisher et al., 1992; Fadely et al.[1]). Rosen and Trites (2000a) found that the fecal digestive efficiency of captive Steller sea lions fed herring, pollock, salmon, and squid was positively correlated with the energy density of their diet. We therefore fitted a logistic equation to the data in Rosen and Trites (2000a; their Tables 1 and 2) using nonlinear least-squares regression (Nonlin; SYSTAT, Inc., 1992) and used this fitted equation (n=20, r^2=0.75) to calculate fecal digestive efficiency as a function of the energy density of prey:

$$DE_i = \frac{A}{1+e^{-k(ED_i - ED_0)}},$$

where DE_i = fecal digestive efficiency for prey category i;
A = 0.951 (±0.0039 SE);
k = 1.86 (±0.016);
ED_i = energy density of prey category i (kJ/g wet mass); and
ED_0 = 2.10 (±0.089).

The fitted parameters (A, k, and ED_0) were randomly sampled from normal distributions with the previously described means and SEs (in each run of the model).

Winship et al. (2002) defined the heat increment of feeding for maintenance as the proportion of metabolizable energy used for maintenance that is lost due to the metabolic cost of digesting and processing food energy, and used a uniform sampling distribution of 0.10–0.15. However, there is evidence that the heat increment of feeding in Steller sea lions, like fecal digestive efficiency, varies with the energy density of prey (Rosen and Trites, 1997; 1999; 2000b). We fitted a linear equation to the data from Rosen and Trites (1997; their Table 1, including data for both meal sizes) and the raw data (Rosen[2]) from Rosen and Trites (1999) and Rosen and Trites (2000b) using linear least-squares regression and used this equation (n=22, P<0.0001, r^2=0.60) to calculate heat increment of feeding as a function of the energy density of prey:

$$HIF_i = a \times ED_i + b,$$

where HIF_i = heat increment of feeding for prey category i (as proportion of gross energy);
a = –0.013 (±0.0023 SE); and
b = 0.229 (±0.0173).

The fitted parameters (a and b) were randomly sampled from normal distributions with the previously described means and SEs (in each run of the model). HIF was then divided by fecal and urinary digestive efficiency to obtain the heat increment of feeding as a proportion of metabolizable energy (Winship et al., 2002).

Population parameters

We used the same sampling distributions for population composition parameters (survival, maturity, and reproductive rates) as outlined in Winship et al. (2002). The sampling distributions for population composition parameters used by Winship et al. (2002) were based on life tables developed for Steller sea lions (York, 1994, Trites and Larkin[3]) that were based on collections done in the 1970s in Alaska (Calkins and Pitcher, 1982). Those life tables were developed on the assumption of a stable population size. However, since the 1970s the sizes of Steller sea lion populations in some regions of Alaska

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[1] Fadely, B. S., J. A. Zeligs, and D. P. Costa. 1994. Assimilation efficiencies and maintenance requirements of California sea lions (*Zalophus californianus*) fed walleye pollock (*Theragra chalcogramma*) and herring (*Clupea harengus*). Final report to the National Marine Mammal Laboratory (NMML), 28 p. NMML, NOAA, 7600 Sand Point Way N. E., Seattle, WA 98115.

[2] Rosen, D. A. S. 2001. Personal commun. Marine Mammal Research Unit, Fisheries Center, University of British Columbia. Room 18, Hut B-3, 6248 Biological Sciences Road, Vancouver, B.C., Canada, V6T 1Z4.

[3] Trites, A. W., and P. A. Larkin. 1992. The status of Steller sea lion populations and the development of fisheries in the Gulf of Alaska and Aleutian Islands. Unpubl. rep., 134 p. Marine Mammal Research Unit, Fisheries Center, University of British Columbia, Room 18, Hut B-3, 6248 Biological Sciences Road, Vancouver, B.C., Canada, V6T 1Z4.

Table 1

Number of Steller sea lion pups counted on rookeries in Alaska in 1998 (Sease and Loughlin, 1999) and minimum total breeding season population size estimates (including pups), assuming pups represent 20.5% of the population (Winship et al., 2002). Areas are defined in Figure 1.

Area	Number of rookeries	Geographic range	Pup count	Population size
Southeast Alaska	3	Forrester–White Sisters	4234	20,669
Gulf of Alaska	9	Seal Rocks–Chernabura	2971	14,503
Eastern Aleutian Islands	6	Pinnacle Rock–Akutan	2340	11,423
Central Aleutian Islands (subarea 1)	8	Bogoslof–Kasatochi	1297	6332
Central Aleutian Islands (subarea 2)	8	Adak–Ayugadak	1729	8440
Central Aleutian Islands (subarea 3)	3	Kiska–Buldir	355	1733
Western Aleutian Islands	3	Agattu–Attu	681	3324
All	40	Forrester–Attu	13,607	66,425

have declined dramatically (Loughlin et al., 1992; Trites and Larkin, 1996). Thus, it is unlikely that population structure was the same in the 1990s as it was in the 1970s and that population structure was the same in all regions of Alaska. Unfortunately, there are very few data available with which to determine the relationship between the structure and the rate of change in size of a population of Steller sea lions. To account for this uncertainty Winship et al. (2002) used sampling distributions for survival, maturity, and reproductive rates that approximated the uncertainty in population structure (ranges of sampling distributions were about 10–20%).

The population size during the breeding season in each region of Alaska was estimated by using pup count data from the U.S. National Marine Fisheries Service and Alaska Department of Fish and Game surveys done in June and July 1998 (Table 1; Sease and Loughlin, 1999). We assumed that the actual number of pups born could have been as much as 20% greater than the number counted because of pups that were hidden during the surveys, pup mortality before the survey dates, and births after the survey dates (Trites and Larkin, 1996). The number of pups in each region was therefore assumed to range from the values in Table 1 to 1.2 × these values (uniform sampling distributions). Total population size was estimated by dividing the number of pups by the proportion of the total population size that they represented as described by Winship et al. (2002).

Diet parameters

Prey species were grouped into seven prey categories as defined by Merrick et al. (1997): 1) cephalopods: squid and octopus; 2) flatfish: Pleuronectidae; 3) forage fish: Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), eulachon (*Thaleichthys pacificus*), and capelin (*Mallotus villosus*); 4) gadids: walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and other Gadidae, 5) hexagrammids: Atka mackerel (*Pleurogrammus monopterygius*) and other Hexagrammidae; 6) salmon: Pacific salmon (*Oncorhynchus* spp.); and 7) other: rockfish (*Sebastes* spp.), sculpins (Cottidae), pricklebacks (Stichaeidae), skates (*Raja* spp.), lamprey (*Lampetra* spp.), sharks, and other demersal fish.

The diet composition of Steller sea lions in southeast Alaska was estimated from data reported by Trites and Calkins[4] for scat collected in the 1990s on rookeries during the summer breeding season and on nonbreeding haulouts (in inside waters) during the rest of the year (Table 2). Split-sample frequencies of occurrence (Olesiuk et al., 1990) of prey categories were used as the median percent contributions of each prey category to diet biomass. Four seasonal diet compositions were used: a "winter" diet commencing on 1 December, a "spring" diet commencing on 1 March, a "summer" diet commencing on 1 June, and an "autumn" diet commencing on 1 September. In order to make the modeled transitions between seasonal diets more gradual, the season dates were sampled from uniform distributions with upper and lower limits equal to ±1 week. It was assumed that all ages and both sexes had the same diet composition.

Diet compositions for Steller sea lions in all other regions of Alaska (Gulf of Alaska–western Aleutian Islands) were estimated from data reported by Merrick et al. (1997) for scats collected mainly on breeding rookeries during the summers of the early 1990s (Table 2). As with southeast Alaska, split-sample frequencies of occurrence were used as the median percent contributions of each prey category to diet biomass. We assumed the same diet composition for all ages and both sexes year-round in these regions. The only area not covered by Trites and Calkins[4] and Merrick et al. (1997) was the eastern Gulf of Alaska. We assumed that the diet composition of Steller sea lions in the eastern Gulf of Alaska was the same as the diet of Steller sea lions in the Gulf of Alaska region from Merrick et al. (1997).

We randomly sampled the diet from triangular distributions to incorporate uncertainty in the diet composition

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[4] Trites, A. W., and D. G. Calkins. 2002. Unpubl. data. Department of Zoology and Marine Mammal Research Unit, Fisheries Center, Univ. British Columbia, Room 18, Hut B-3, 6248 Biological Sciences Road, Vancouver, B.C., Canada, V6T 1Z4.

Table 2

Diet composition (median percent biomass contribution of each prey species category in the diet) of Steller sea lions in Alaska. Values for southeast Alaska are based on split-sample frequency of occurrence data from Trites and Calkins,[4] and values for the Gulf of Alaska through the western Aleutian Islands are based on split-sample frequency of occurrence data from Merrick et al. (1997). Prey categories are defined in the text and areas are defined in Figure 1.

	Prey category						
Area	Cephalopods	Flatfish	Forage fish	Gadids	Hexagrammids	Other	Salmon
Southeast Alaska							
Winter (Dec–Feb)	8.1	7.6	13.5	49.1	0.0	20.4	1.2
Spring (Mar–May)	5.0	7.6	21.0	52.5	0.0	12.5	1.4
Summer (Jun–Aug)	0.8	6.4	21.9	27.3	0.4	16.0	27.3
Autumn (Sep–Nov)	7.0	6.2	12.5	62.2	0.1	8.8	3.3
Gulf of Alaska	2.9	3.9	6.1	66.5	0.3	0.0	20.3
Eastern Aleutian Islands	2.3	1.8	7.7	32.9	30.7	7.3	17.3
Central Aleutian Islands (subarea 1)	0.0	0.0	3.3	40.2	29.4	5.4	21.8
Central Aleutian Islands (subarea 2)	13.7	0.0	0.0	9.7	69.7	2.2	4.7
Central Aleutian Islands (subarea 3)	7.1	0.0	0.0	3.2	84.2	4.9	0.5
Western Aleutian Islands	6.7	0.0	0.0	6.9	77.3	4.6	4.6

(percentage of biomass that each prey category represented in the diet). These distributions had medians from Table 2 and upper and lower limits equal to ±45% of medians ≥10%, or ±98% of medians <10%. These percentages were then standardized so that all prey categories were summed to 100% for a given diet. The ranges of the assumed errors in diet composition were determined by using estimates of the minimum and maximum split-sample frequencies of occurrence of prey categories (Olesiuk et al., 1990; Olesiuk, 1993; see "Discussion" section).

The energy density of fish is a function of their chemical composition, especially their lipid content (Stansby, 1976; Hartman and Brandt, 1995). Thus, the energy density of fish can vary with age (older fish tend to store more lipid; Brett, 1983; Harris et al., 1986; Paul et al., 1998a), season (lipid content can vary with foraging conditions; Paul et al., 1993; Paul et al., 1998a; Robards et al., 1999), reproductive status (lipid content of spawning fish can be different from nonspawning fish; Dygert, 1990; Smith et al., 1990; Hendry and Berg, 1999), and geographic location (feeding conditions can vary with location; Paul and Willette, 1997; Lawson et al., 1998; Paul et al., 1998b). The quantity and resolution of data on the energy density of prey of Steller sea lions varied depending on the prey species (Appendix I). When detailed season-specific energy-density data were available for prey species, we generally incorporated seasonal changes in energy density. Unfortunately, no detailed geographic-specific energy density data were available for any prey species; therefore we assumed that the energy density of prey did not vary among regions of Alaska. We used relatively wide ranges of possible energy-density values for all prey in order to incorporate the uncertainty in how energy density varies with season and geographic location.

Many data were available on the energy density of forage fish (Appendix I). The energy densities of forage fish species are relatively high, but vary seasonally in relation to spawning periods, the over-winter fast, and spring and autumn phytoplankton blooms (Anthony et al., 2000). For example, eulachon had a very high energy density (7.5–11.1 kJ/g wet mass) and its energy density was slightly higher in the summer than in late winter (Payne et al., 1999). The energy density of capelin was lower, ranging from 3.5 to 7.0 kJ/g wet mass. In the Gulf of Alaska, the energy density of capelin was high in June (start of spawning) after the spring phytoplankton bloom and decreased through the summer with advancing reproductive stage (Anthony et al., 2000). The energy density of capelin increases again in the fall and early winter as the fish feed on the autumn phytoplankton bloom (Lawson et al., 1998; Payne et al., 1999; Anthony et al., 2000).

Pacific herring and Pacific sandlance were the two main forage fish species consumed by Steller sea lions in Alaska in the 1990s (Merrick et al., 1997, Trites and Calkins[4]). The energy density of Pacific herring increased with age, and the energy density of adults (age >0) ranged from 4.4–11.7 kJ/g wet mass (Appendix I). In the Gulf of Alaska, Pacific herring were highest in energy content in the autumn and lowest in energy content in the spring (after the overwinter fast; Paul et al., 1998a), but the exact timing of these seasonal changes varied depending on the region of Alaska (Perez, 1994). Pacific sandlance (age >0) ranged in energy density from about 3.2 to 6.1 kJ/g wet mass. Pacific sandlance from the Gulf of Alaska was highest in energy content in June (after the spring bloom), and its energy content decreased through autumn (spawn mid-autumn) and remained low throughout the winter fasting period (Robards et al., 1999; Anthony et al., 2000). We assumed the energy density of the forage fish prey category was 4.9–11.7 kJ/g in the summer and autumn, and 3.2–6.3 kJ/g in the winter and spring.

Gadids consumed by Steller sea lions in Alaska in the 1990s were primarily walleye pollock, but Pacific cod was also an important prey species (Merrick et al., 1997, Trites and Calkins[4]). The energy density of walleye pollock increases with age, and the energy density of pollock in the size range primarily consumed by Steller sea lions (age>0, range 5–65 cm; Pitcher, 1981, Calkins 1998, Calkins and Goodwin[5]) ranged from about 3.2 to 5.9 kJ/g (Appendix I). The data in Appendix I do not suggest that walleye pollock undergo marked seasonal changes in energy density in Alaska. Pacific cod (age>0) was similar in energy density to walleye pollock and ranged from about 3.3 to 4.5 kJ/g (Appendix I). However, Smith et al. (1990) found that adult Pacific cod had a relatively high energy density in early spring (ripe, prespawning), declined to a low energy density in the summer (postspawning), and then increased to a high energy density again by early winter. Because the energy density of Pacific cod throughout the year was within the range of the energy density of walleye pollock, we assumed that the energy density of the gadid prey category was constant year-round and equal to 3.2–5.9 kJ/g.

Flatfish species from the northeast Pacific Ocean had energy densities ranging from approximately 2.9 to 6.0 kJ/g (Appendix I). Two species, English sole (*Parophrys vetulus*) and yellowfin sole (*Pleuronectes asper*), exhibited seasonal changes in energy density. The energy density of adult female English sole increased from spring through mid-autumn (feeding and energy storage period) and decreased thereafter (Dygert, 1990). Juvenile and adult yellowfin sole increased rapidly in energy density at the beginning of summer (June, spawning period), and energy density then decreased through the following spring (Paul et al., 1993). Dygert (1990) and Paul et al. (1993) have suggested that these seasonal patterns of energy density are common for most northern flatfish species. We assumed the energy density of the flatfish prey category was 4.0–6.0 kJ/g in the summer and autumn and 2.9–4.9 kJ/g in the winter and spring.

The primary factors affecting the energy density of Pacific salmon are size and age (Appendix I). The data in Appendix I do not indicate substantial seasonal variability in the energy density of Pacific salmon. Energy density increases with size until salmon return to freshwater and spawn—at which point energy density drops drastically (Brett, 1983; Hendry and Berg, 1999). Steller sea lions in Alaska consumed salmon approximately 25–60 cm in length (Trites and Calkins[4]), which we assumed corresponded to a range in mass of approximately 0.3–3 kg, and an energy density ranging from about 6.1 to 8.7 kJ/g.

Hexagrammids were a major component of the diet of Steller sea lions in the western regions of Alaska during the 1990s (Table 2). The main hexagrammid species consumed was Atka mackerel (Merrick et al., 1997). Unfortunately, very few data are available on the energy density of Atka mackerel. Juvenile hexagrammids (≤12 cm), including Atka mackerel, have energy densities ranging from about 3.5 to 4.7 kJ/g (Appendix I). However, Steller sea lions likely consume fish longer than 12 cm, which may have higher energy densities. We therefore assumed the energy density of the hexagrammid prey category was 3.5–6.0.

Detailed seasonal and size-specific data on the energy density of cephalopods and other fish species were not available. We assumed (from the data in Appendix I) that the energy densities of the cephalopod and "other" prey categories were 3.8–6.5 kJ/g and 3.1–6.9 kJ/g, respectively.

Results

Seasonal food requirements (southeast Alaska)

Predicted seasonal changes in gross energy requirements of Steller sea lions in southeast Alaska (per individual) were largely driven by changes in activity budgets (Fig. 2; Winship et al., 2002). Immature animals and mature males were assumed to have relatively constant activity budgets and therefore had relatively constant daily energy requirements. The exception was a drop in the energy requirements of mature males during the breeding season. Energy requirements of mature females were also lowest during the breeding season and generally increased from summer through the following spring, especially if females were pregnant. The energy required to nurse a pup increased steadily throughout the pup's first year of life.

A small part of the seasonal change in gross energy requirements of all animals other than pups can be attributed to variation in the energy density of prey and associated differences in digestive efficiency and the heat increment of feeding. The summer diet had the largest proportions of prey species with high energy densities (forage fish and salmon), and therefore had a higher overall energy density than the autumn, winter, and spring diets (Table 2). Thus, digestive efficiency was highest and the heat increment of feeding was lowest in the summer. The winter and spring diets in southeast Alaska had a lower energy density due to the higher proportions of species with low energy densities and because flatfish and forage fish were assumed to have a lower energy density during winter and spring. As a result, digestive efficiency was lower and the heat increment of feeding was higher during the winter and spring than during the summer. The energy density of the autumn diet (and digestive efficiency and the heat increment of feeding) was intermediate between the energy densities of the summer diet and the winter and spring diets. These seasonal changes in efficiency resulted in up to 4% increases in gross energy requirements during the autumn, winter, and spring in

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[5] Calkins, D. G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Unpubl. rep., 76 p. Alaska Department of Fish and Game, Division of Wildlife Conservation, 333 Raspberry Road, Anchorage, AK 99518-1599.

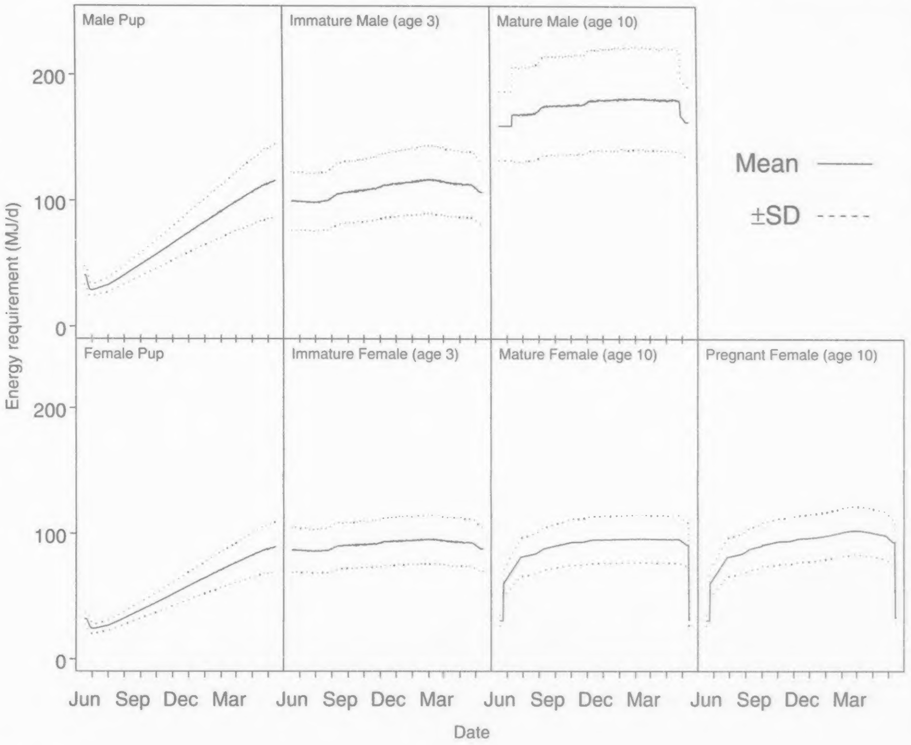

Figure 2

Gross energy requirements of individual Steller sea lions by day of the year. Pup energy requirements represent the amount of energy a female would require to support an entirely dependent pup (i.e. they include energy lost by the mother as waste and the inefficiency of milk synthesis). SDs were obtained by using Monte Carlo simulations (1000 runs). We assumed the date of birth was 15 June. Note that these are plots of energy requirements, not energy consumption. For example, mature males do not consume energy during the breeding season fast (late May–early July).

relation to summer (independent of seasonal changes in metabolizable energy requirements).

Estimated seasonal changes in food requirements in southeast Alaska during the 1990s (Fig. 3) were more pronounced than seasonal changes in energy requirements (Fig. 2) because seasonal changes in the energy density of the diet resulted in large seasonal changes in the amount of food biomass required per unit of gross energy. In general, food requirements were highest in the winter and spring when the energy density of the diet was lowest. Food requirements were lowest in the summer when the energy density of the diet was highest, and food requirements in the autumn were intermediate between those of summer and winter–spring. The maximum daily food requirements in southeast Alaska occurred in March when immature 3-year-old males and females required 25 (±6.9 SD) kg and 21 (±5.2) kg respectively, and mature 10-year-old males and nonpregnant females required 39 (±10.4) kg and 21 (±5.0) kg, respectively. The maximum daily food requirement for a pregnant 10-year-old female nursing a pup averaged 40–46 kg (mid-May). In comparison, daily food requirements in summer, just after the breeding season (1 August), were only 62–69% of these maximum food requirements (immature 3-year-old male: 16 [±4.0] kg, immature 3-year-old female: 14 [±3.1] kg, mature 10-year-old male: 27 [±6.7] kg, mature nonpregnant 10-year-old female: 13 [±2.8] kg). A mature female nursing a pup required only an average of 17–18 kg of food per day at this time of year (39–43% of her maximum daily food requirement).

Regional food requirements

Total annual population food requirements in 1998 varied among regions, as expected because of differences in diet and population size (Fig. 1). When annual food requirements were estimated with diet information from summer only, the model predicted that the southeast Alaska popu-

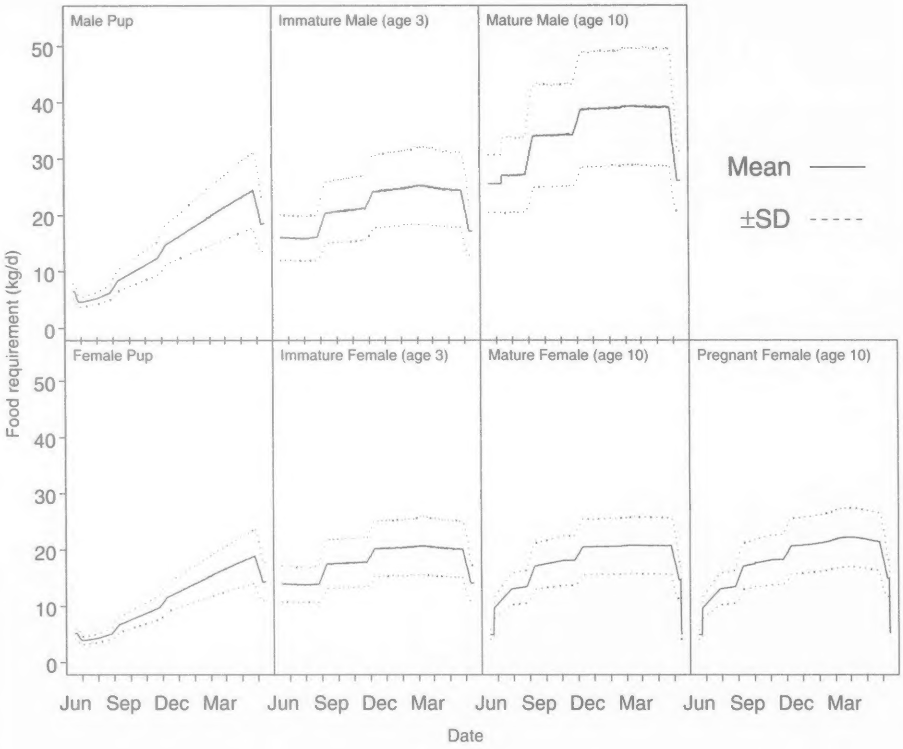

Figure 3

Food biomass requirements for individual Steller sea lions in southeast Alaska by day of the year. Pup food requirements represent the amount of food a female would require to support an entirely dependent pup. SDs were obtained by using Monte Carlo simulations (1000 runs). We assumed the date of birth was 15 June. Note that these are plots of food requirements, not food consumption. For example, mature males do not consume food during the breeding season fast (late May–early July).

lation consumed the most prey biomass on an annual basis (121,000 [±23,300] t) and the central Aleutian Islands 3 population consumed the least (12,500 [±2470] t). The large difference in total consumption primarily reflects the large difference in population size between regions. For southeast Alaska, the only region where diet information was available for all four seasons, the estimated prey biomass consumed on an annual basis increased from 121,000 (±23,300) t (assuming a summer diet all year) to 140,000 (±27,800) t (when diet changed seasonally) because of higher proportions of low–energy-density prey in the diet (and therefore lower energy density of the diet) in autumn, winter, and spring (Table 2). The CVs of total annual population food biomass consumption were 19–20%.

Based on summer diets, the predicted average daily food requirement per individual (all ages) ranged from 16 (±2.8) kg (southeast Alaska) to 20 (±3.6) kg (central Aleutian Islands [subarea 3])—a 24% difference (Fig. 4). The average daily per capita food requirement for southeast Alaska increased by 3 kg (to 19 [±3.4] kg) when the diets for all four seasons were considered. In general, per capita food requirements were lowest in regions where Steller sea lions consumed high proportions of high–energy-density prey (forage fish and salmon), as in the eastern Aleutian Islands and central Aleutian Islands (subarea 1), and were highest in regions where the diet contained larger proportions of low–energy-density prey (gadids and hexagrammids), as in the western Aleutian Islands and central Aleutian Islands (subareas 2 and 3).

The greatest estimated consumption of a single prey species category in a region in 1998 was 68,600 (±14,400) t of gadids in southeast Alaska (using diet information for all seasons; Fig. 5). Gadids were consumed in a similar amount in the Gulf of Alaska (62,700 [±12,800] t). Alaska-wide, the top two prey categories in terms of biomass consumption were gadids and hexagrammids (gadids – 179,000 [±36,700] t, hexagrammids – 104,000 [±20,600] t). The Steller sea lion population in the central Aleutian Islands (subarea 2) (Fig. 1) consumed the most hexagram-

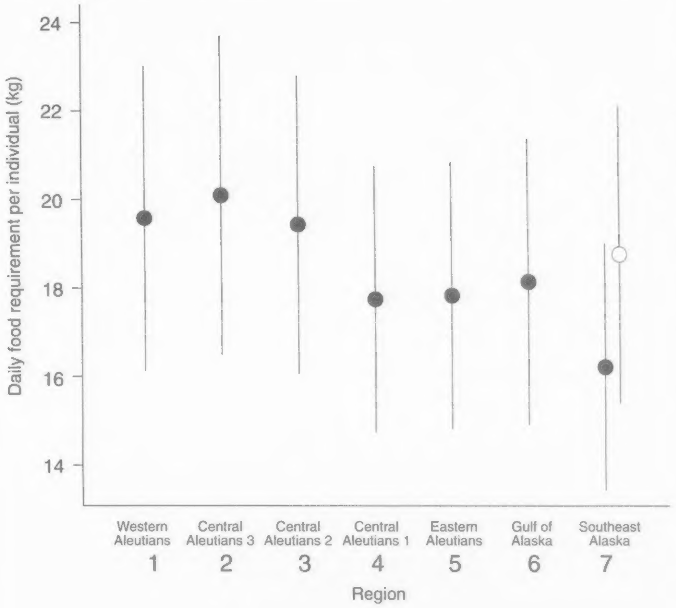

Figure 4

Estimated average daily food biomass requirements per individual Steller sea lion (all ages combined) from seven regions of Alaska based on summer diet information (filled circles). For southeast Alaska, the estimated per capita food requirement based on diet information for all four seasons is also shown (unfilled circle). Error bars represent ±1 SD (obtained by using Monte Carlo simulations–1000 runs).

mid biomass of any region (41,000 [±8070] t). CVs of individual prey category consumption ranged from 20 to 39%.

Discussion

Uncertainty in model predictions

An important aspect of our model is that it produces distributions of predicted food requirements rather than point estimates (Winship et al., 2002). This allowed us not only to estimate mean predicted food requirements but also to estimate the potential error in these mean predictions by using either SD or CV (SD as a percentage of the mean). We found that the CVs of mean predicted food requirements at the population level (both total biomass and individual prey categories) were approximately 20–40%. The ranges of food requirements predicted by the model were of course much wider than ±1 CV. For instance, 5% of the predicted values lie beyond ±1.96 CV if the normal distribution is used to approximate the distribution of model predictions. The minimum and maximum food requirement estimates predicted by the model were generally <40% of the mean and >160% of the mean, respectively, if the CV of the mean predicted food requirement was 30%. Thus, the ranges of predictions produced by our model reflect considerable uncertainty in the food requirements of Steller sea lions because of the assumed errors that we attributed to certain bioenergetic parameters (e.g. metabolic rate at sea), population parameters (e.g. age- and sex-specific survival rates), and diet parameters (e.g. diet composition). Future research on key parameters in our model will help to refine the predictions of this model and improve the accuracy of estimates of the food requirements of this species.

Biases in diet composition

The diet compositions that we used were estimated from the hard parts of prey found in scats collected on haul-outs and rookeries and were limited by incomplete sampling coverage by time of the year and by sex- and age-class. Diet data from the western Aleutian Islands through the Gulf of Alaska came mainly from mature females on breeding rookeries during late June, early July, and early August in the early 1990s (Merrick et al., 1997). Thus, these data reflect a specific segment of the population during a short period of the year.

We applied the diets reported by Merrick et al. (1997) to all age- and sex-classes of Steller sea lions in 1998 and assumed that those diets did not change seasonally. Data reported by Sinclair and Zeppelin (2002) suggest that the dominant prey in more recently collected samples from the Gulf of Alaska and Aleutian Islands in summer (breeding females on rookeries) and winter (juvenile and adult males and females on nonbreeding haul-outs) were similar to those reported by Merrick et al. (1997). Sinclair and Zeppelin (2002) found walleye pollock more frequently than any other prey species in Steller sea lion scats from the Gulf of Alaska and eastern Aleutian Islands during the summer and winter, whereas Atka mackerel was the second most frequently occurring prey species in the eastern Aleutian Islands, and the most frequently occurring prey species in the central and western Aleutian Islands during summer and winter. However, Sinclair and Zeppelin (2002) did find significant seasonal changes in the frequency of certain prey species in the diets of Steller sea lions at specific sites in Alaska. For example, Pacific cod occurred more frequently in scats collected on haul-outs during the winter than in scats collected on rookeries during the summer in all regions (Gulf of Alaska through western Aleutian Islands). Pacific salmon occurred more frequently in the summer than in the winter in the Gulf of Alaska and the eastern Aleutian Islands, while this seasonal difference was reversed in the central and western Aleutian Islands. A seasonal change in the proportion of the diet comprising high-energy prey species like salmon can have a substantial effect on the total and per capita amount of food biomass required by Steller sea lions (e.g. our results for southeast Alaska). Nevertheless, given the similarities between the two summer and winter data sets (from Sinclair and Zeppelin, 2002, and Merrick et al., 1997), and given the level of uncertainty that we incorporated in our diet compositions, we feel that the diet compositions that we assumed for Steller sea lions in the western Aleutian Islands through Gulf of Alaska regions in 1998 were reasonable approximations.

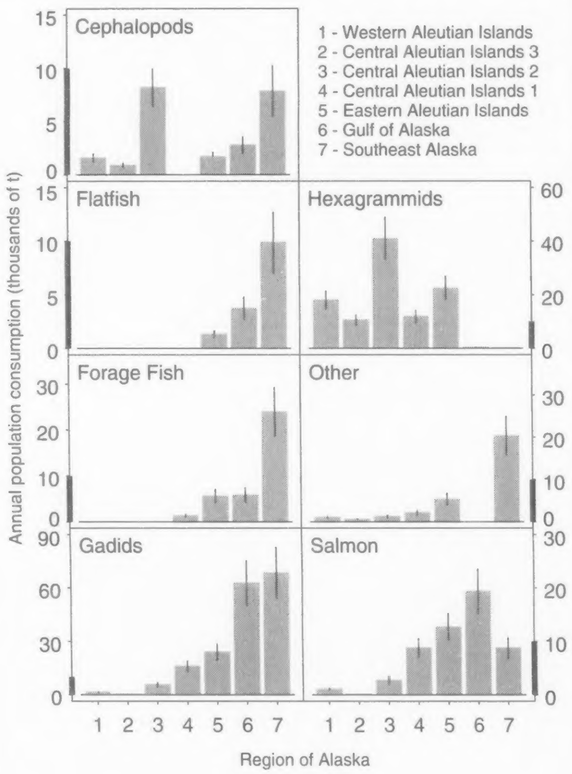

Figure 5

Annual prey biomass consumption for Steller sea lions in 1998 in the seven study areas of Alaska. Values for southeast Alaska were estimated by using diet information for all four seasons. Error bars represent ±1 SD (obtained by using Monte Carlo simulations–1000 runs).

The scat data we used to estimate the diet of Steller sea lions in southeast Alaska had better temporal and demographic coverage. Trites and Calkins[4] reported data from scats collected in every month except September. Although the scat data from the summer months were again from breeding females on rookeries, the scat data from the rest of the year were from nonbreeding animals on haul-outs. Animals using these haul-outs included adult and juvenile males and females. Thus, those scats were more representative of the average diet of the population than scats collected on rookeries during the breeding season. There is evidence that the diet of mature females on rookeries differs from the diet of nonbreeding animals on haul-outs during the summer (Trites and Calkins[4]), but it is difficult to translate this difference into sex- or age-specific dietary differences.

In addition to sampling limitations, there are at least two other potential biases associated with using scat data to assess diet composition. The first potential bias is the possibility that some of the consumed prey species were not represented in the scat samples (Bowen, 2000). Although the identification of prey hard parts other than otoliths in scats increases the probability of detection of prey species, cartilaginous fish or fish with small or fragile bony structures may be completely digested and not evident in scat (Olesiuk et al., 1990). For example, in captive Steller sea lion feeding trials, the average number of hard parts recovered in scat was 31.2 per pollock, but only 7.9 per herring (Cottrell and Trites, 2002). Thus, there was a greater chance of an individual herring being missed compared to an individual pollock. However, small fish are likely consumed in larger numbers, which would increase the likelihood of detecting their presence in scat.

The second potential source of dietary bias arises from using the "split-sample frequency of occurrence" technique to estimate the percentage of biomass that different prey represent in the diet. This technique assumes that the prey identified in a scat sample represent all the prey consumed in a meal, and that all prey species of a meal are consumed in equal biomasses (Olesiuk et al., 1990). This method may overestimate the contribution of small prey and underestimate the contribution of large prey to diet biomass. However, as previously mentioned, such a bias would be reduced if small prey are consumed in greater numbers than large prey in a given meal. A potentially better technique than split-sample frequency of occurrence is volumetric or biomass reconstruction analysis (i.e. the estimation of the actual size of each prey in a scat from the size of otoliths or other hard parts), but otoliths are usually not available from Steller sea lion scat (Merrick et al., 1997) and digestion correction factors (Tollit et al., 1997) and regressions of hard-part size on body size are currently not available for prey of Steller sea lions.

Olesiuk et al. (1990) and Olesiuk (1993) estimated the error associated with a key assumption of the split-sample frequency of occurrence technique (all prey categories in a scat are consumed in equal quantities) by calculating the minimum and maximum split-sample frequencies of occurrence of prey. For example, the minimum split-sample frequency of occurrence of a prey category was calculated by assuming that when the prey category was found in a scat with another prey category, it represented a negligible proportion of the biomass of the meal represented by that scat. We considered their estimates of the minimum and maximum split-sample frequencies of occurrence of prey to approximate the total potential errors in the diet compositions we used. Thus, the assumed errors in diet were based only on the potential error in estimating diet from scats and not on the potential error due to sampling limitations.

Our assumed errors in diet composition were relatively large. For example, if a prey category was assumed to comprise a median of 50% of the diet, the proportion of the diet represented by that prey category in any one run of the model ranged from 27.5% to 72.5% (before the diet was standardized to 100%). Nevertheless there is still the possibility of sampling biases in the diet compositions that we assumed for Steller sea lions in Alaska. Future studies of the diet of Steller sea lions will allow us to obtain better estimates of the regional, seasonal, and intrapopulation variability in diet. Also, studies of captive Steller sea lions will assist in determining the biases and variability associated with the estimation of diet from scats (Cottrell and Trites, 2002).

Effect of diet on food requirements

We found that changes in the energy density of the diet can have large effects on the amount of food that Steller sea lions need to consume. In southeast Alaska, seasonal changes in the energy density of the diet resulted in large seasonal changes in daily food requirements, even when daily energy requirements were relatively constant. Immature and mature animals (excluding lactating females) required approximately 45–60% more food per day in early spring than in late summer (Fig. 3). Regional differences in the energy density of the diet resulted in smaller, but still substantial differences in food requirements among Steller sea lions in different regions of Alaska (up to a 24% difference based on summer diets).

The effect of diet on food requirements, can be further illustrated by considering two diets: one of entirely gadids (walleye pollock, Pacific cod) and one of entirely small schooling fish (herring, sandlance). Based on caloric differences between prey types and differences in digestive efficiency and the heat increment of feeding, a 10-year-old male would require an average of 30 (±7.7) kg of small schooling fish per day (5% of body mass), but would require 41 (±9.7) kg of gadids (6% of body mass): a 37% increase in prey biomass requirements. A 10-year-old female's (pregnant, no pup) average daily food requirement would increase by a similar percentage with a diet shift from small schooling fish to gadids (15 [±3.7] kg to 21 [±4.7] kg or 6% to 8% of body mass).

A large animal may be able to compensate for changes in prey biomass requirements, but immature or recently weaned animals may be more susceptible to changes in prey biomass requirements because they need to consume more food per unit body mass than adult animals (Winship et al., 2002). A 1-year-old male would require an average of 16 (±4.2) kg of small schooling fish per day (12% of body mass), but would require an average of 22 ±5.4 kg of gadids (16% of body mass). Similarly, a 1-year-old female would need 14 (±3.2) kg of small schooling fish (13% of body mass) or 18 (±4.1) kg of gadids (17% of body mass). The difference in energy density between the gadid and forage fish categories was greater in the summer and autumn than in the winter and spring; thus the difference between the daily food requirement of a sea lion consuming only gadids and the food requirement of a sea lion consuming only forage fish was greatest in the summer and autumn. Although animals prey on more than one species category in nature, which would buffer the effects of changes in diet composition, differences in the energy density and digestibility of prey can have large effects on prey biomass requirements, especially for young animals.

Merrick et al. (1997) found a significant relationship between the diversities of Steller sea lion diets and the rates of change in the numbers of adult and juvenile Steller sea lions counted on rookeries between 1990 and 1994 in different regions of Alaska (Gulf of Alaska through the western Aleutian Islands). Sea lions in regions with high rates of population decline had low dietary diversity. Plotting the rates of population decline against the amount of prey required in each region (using summer diets), we found a significant (α=0.05) relationship (Spearman rank correlation coefficient r_s=–0.929, P=0.02; Fig. 6), indicating that sea lions in areas with high rates of decline had higher per capita food requirements. This finding suggests that the energy density of the diet may have had a role in the population decline in some regions of Alaska during the early 1990s.

The correlation we report between food requirements and population change (Fig. 6) is based on summer diets and limited data on the energy density of sea lion prey categories such as hexagrammids. When seasonal diet information for southeast Alaska was considered, our model predicted a substantially greater per capita food requirement in that region (Fig. 4). Seasonal data are required from all regions of Alaska to describe diet composition

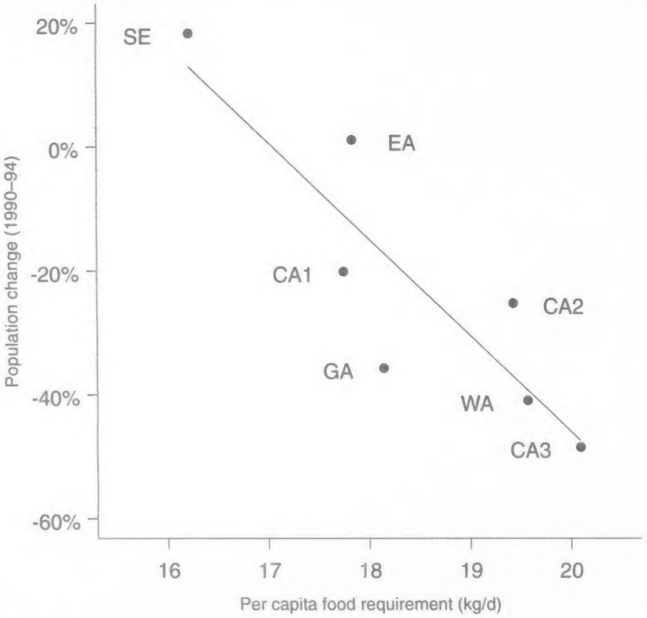

Figure 6

Per capita daily food biomass requirement predicted by our model (based on summer diets) versus rate of change in the number of adult and juvenile Steller sea lions counted on rookeries between 1990 and 1994 by region of Alaska (SE=Southeast Alaska, GA=Gulf of Alaska, EA=Eastern Aleutians, CA=Central Aleutians, WA=Western Aleutians). The Spearman rank correlation coefficient (r_s) for the data is –0.929 (P=0.02). The line represents a linear least-squares regression (r^2=0.77). Data on population change are from Merrick et al. (1997), except the value for southeast Alaska (18.3%) which we calculated from data reported by Strick et al. (1997) for three rookeries (Forrester, Hazy, and White Sisters islands).

and energy density, so that the potential relationship between rates of population change and per capita food requirements can be fully explored. Nevertheless, the data that are currently available are intriguing and suggest a possible mechanism for the original relationship reported by Merrick et al. (1997) between diet diversity and population decline.

Steller sea lions may use a couple of strategies to respond to increases in food requirements. The first and obvious strategy is to increase the rate of food intake. Many studies have found that animals increase their food intake on low-energy diets (Hammond and Wunder, 1991; Veloso and Bozinovic, 1993; Brekke and Gabrielsen, 1994; Weber and Thompson, 1998). Fadely et al.[1] found that the intake rates of captive California sea lions (*Zalophus californianus*) eating walleye pollock were approximately 1.4 times greater than when consuming herring. In order to increase their rate of food intake, Steller sea lions would likely have to increase the amount of time spent foraging or their activity level while foraging (or would have to do both). An increase in foraging time would likely result in increased pup mortality because mothers would be absent from haul-outs for longer periods of time (Trillmich and Dellinger, 1991; Boyd et al., 1994) or in increased susceptibility of these mothers to predation by killer whales (*Orcinus orca*) or sharks. An increase in foraging intensity may result in an increase in the energy cost of foraging, and therefore additional increases in food requirements (Costa and Gentry, 1986).

A second strategy Steller sea lions may employ to respond to decreases in the energy content of their diet is to reduce energy expenditures and thereby prevent an increase in food biomass requirements. For example, Veloso and Bozinovic (1993) found that degus (*Octodon degus*) eating low-quality forage, had lower basal metabolic rates than degus eating high-quality forage. A similar metabolic depression was observed in captive Steller sea lions eating low-energy squid and walleye pollock (Rosen and Trites, 1999; Rosen and Trites, 2000b). Steller sea lions may also reduce energy expenditures by decreasing their activity levels. Studies of the rifleman (*Acanthisitta chloris*; Lill, 1991) and white-footed sportive lemur (*Lepilemur leuco-*

pus; Nash, 1998) found that animals conserved energy by reducing the time they spent active and by increasing the time they spent resting when energy requirements for thermoregulation increased during cold periods. Mature female Steller sea lions may also have an additional option of reducing energy investment in reproduction by aborting fetuses to conserve energy during periods of nutritional stress (Pitcher et al., 1998).

Steller sea lions consuming very low–energy-density diets may be unable to consume enough food biomass to meet even reduced energy requirements. This situation could result from prey handling and digestion-time constraints or from an inability to capture enough prey. Juvenile animals would likely be the most susceptible to both situations. As discussed, juvenile animals have much higher mass-specific food requirements, and young animals may not be able to process 16–17% of their body weight in food per day (mean daily food requirements of 1-year-olds on a strictly gadid diet). Juvenile animals may also experience diving constraints (e.g. dive depth; Merrick and Loughlin, 1997) that adults do not, and may have more difficulty capturing sufficient quantities of low-energy prey.

An important consideration regarding the effect of diet composition on food requirements is the energetic cost of foraging on different prey species. Differences in the size and behavior of individual prey items may reduce differences in food biomass requirements resulting from differences in the energy density of prey. For example, consider a situation where a Steller sea lion can consume either small herring of high energy density or large pollock of low energy density. To obtain a given amount of prey biomass the sea lion can consume either several small herring or one large pollock. Based on the energy density of the prey, the sea lion would acquire a greater absolute amount of energy from the herring than from the pollock. However, if the energetic cost of pursuing and capturing several herring was greater than the cost of pursuing and capturing one pollock, then the net amount of energy obtained (energy consumed minus energy spent) per unit of prey biomass may not differ between the herring and the pollock diets. In other words, the sea lion's food requirement would be similar whether it was foraging on the small herring or the large pollock.

We did not incorporate differential costs associated with foraging on different prey categories in our model. We also did not consider the size of individual prey items consumed by Steller sea lions. Data on foraging costs for Steller sea lions in relation to prey species and prey size are currently limited and should be incorporated into bioenergetic models as they become available, in the form of functional relationships between diet composition and the energetic cost of foraging.

Prey consumption by Steller sea lions in Alaska in 1998

Regional variation in the amount of prey consumed by Steller sea lions in Alaska in 1998 (Figs. 1 and 5) was mainly due to differences in population size, as well as differences in diet composition (previous section). Gadids and hexagrammids were the top two prey categories in terms of biomass consumed. Gadids dominated the diet in the eastern areas (Gulf of Alaska), whereas hexagrammids dominated the diet in the western areas (central Aleutians 2 to western Aleutians). Gadids also dominated the diet in southeast Alaska when considered on an annual basis.

The mean model estimate of gadid consumption by Steller sea lions in all study regions of Alaska in 1998 was 179,000 (±36,700) t per year. This represents about 7% of the total estimated walleye pollock biomass, 20% of the total estimated Pacific cod biomass, or 5% of combined pollock and cod biomass dying naturally in 1998 in the Gulf of Alaska, Aleutian Islands, Bogoslof area, and eastern Bering Sea (Table 3). Steller sea lion consumption of gadids also represents 12% of the total gadid biomass removed in 1998 by commercial fisheries. Thus, estimated total gadid biomass consumption by Steller sea lions in Alaska is less than that taken by the fishery, and is small in relation to total gadid natural mortality. Livingston (1993) also estimated that the pollock biomass taken by sea lions in the eastern Bering sea in 1985 was small in relation to that taken by the fishery and remarked that cannibalism of adults on juveniles was the greatest source of mortality for walleye pollock.

We estimated that Steller sea lions in all areas of Alaska consumed a total of 104,000 (±20,600) t of hexagrammid biomass in 1998 (75% of estimated exploitable Atka mackerel biomass dying naturally in the Aleutian Islands, and 181% of fishery catches in the Aleutian Islands and the Gulf of Alaska in 1998; Table 3). Thus, Steller sea lions removed more Atka mackerel biomass than the fishery in 1998, and Steller sea lion predation accounted for a large proportion of natural Atka mackerel mortality. However, this proportion would be lower if Steller sea lions also prey on juvenile Atka mackerel. As with gadids, other fish species (e.g. Pacific cod) are also important predators on Atka mackerel (Yang, 1997).

Inferences about prey availability and competition for prey between fisheries and Steller sea lions should be made with caution given that we did not explicitly consider the size of prey in our study. For example, Steller sea lions have been shown to generally prey on juvenile pollock and not consume pollock longer than about 60 cm (Pitcher, 1981; Calkins, 1998; Calkins and Goodwin[5]). Thus, with respect to prey availability it may be more appropriate to compare our estimate of the gadid biomass consumed by Steller sea lions to the biomass of juvenile gadids dying naturally rather than to the total gadid biomass dying naturally. Our estimate of the biomass of gadids consumed by Steller sea lions in Alaska in 1998 represented 18% of the natural mortality of juvenile pollock and cod combined (23% of juvenile pollock alone or 80% of juvenile cod alone), which was more than triple the value (5%) when total pollock and cod biomass was considered (Table 3). The impact of Steller sea lions on specific segments of their prey populations (e.g. juvenile Pacific cod) may then be much greater than the impact that is suggested when only total biomass is considered. With respect to competition with fisheries, the pollock and cod fisheries generally target fish ≥3 years old. Thus,

Table 3

Biomass (t), natural mortality, fishery catches (t), and predicted Steller sea lion consumption of gadids (walleye pollock and Pacific cod) and hexagrammids (Atka mackerel) in Alaska in 1998.

	Walleye pollock	Pacific cod	Gadid (pollock+cod)	Hexagrammid (Atka mackerel)
Adult (age 3+)				
biomass [1]	7,362,000	2,125,000	9,487,000	536,000
M	0.30[2]	0.37[3]		0.30[4]
biomass dying naturally[5]	1,908,096	657,190	2,565,286	138,921
Juveniles				
biomass	1,616,049[6]	466,463[6]	2,082,512	no data
M	0.65[7]	0.65[7]		no data
biomass dying naturally	772,397	222,948	995,345	no data
Total				
biomass	8,978,049	2,591,463	11,569,512	
biomass dying naturally	2,680,493	880,138	3,560,631	
fishery catches[8]	1,250,594	267,968	1,518,562	57,493
Steller sea lion population consumption			179,000 ±36,700	104,000 ±20,600
% total biomass dying naturally	6.7	20.3	5.0	
% adult biomass dying naturally	9.4	27.2	7.0	74.9
% juvenile biomass dying naturally	23.2	80.3	18.0	
% fishery catches	14.3	66.8	11.8	180.9

[1] Sum of estimated exploitable biomass from Gulf of Alaska (pollock and cod only) (Plan Team for the Groundfish Fisheries of the Gulf of Alaska. 1999. Summary. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 1–31. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510), Aleutian Islands, Bogoslof (pollock only), and eastern Bering Sea (pollock and cod only) regions (Plan Team for the Groundfish Fisheries of the Bering Sea and Aleutian Islands. 1999. Summary. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 1–36. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510). Estimate of exploitable biomass of Atka mackerel in the Gulf of Alaska not available, but the population was much smaller than the Aleutian Islands population.

[2] Dorn, M. W., A. B. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn. 1999. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 33–104. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510

[3] Thompson, G. G., H. H. Zenger, and M. W. Dorn. 1999. Assessment of the Pacific cod stock in the Gulf of Alaska. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 105–184. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[4] Lowe, S. A., and L. W. Fritz. 1999. Assessment of Bering Sea/Aleutian Islands Atka mackerel. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 569–638. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[5] Annual mortality rate = $1 - e^{-M}$.

[6] Assumed to be 18% of total biomass based on value used by Trites et al. (1999) for pollock.

[7] Assumed to be the median *M* reported by Wespestad and Terry (1984) for 1- and 2-year-old pollock (range=0.45–0.85).

[8] Sum of catches from Gulf of Alaska (Plan Team for the Groundfish Fisheries of the Gulf of Alaska, see Footnote 1 above), Aleutian Islands, Bogoslof (pollock only), and eastern Bering Sea (pollock and cod only) regions (Plan Team for the Groundfish Fisheries of the Bering Sea and Aleutian Islands, see Footnote 1 above).

there may only be minor overlap between the fish taken by humans and the fish taken by Steller sea lions even though our estimate of the gadid biomass consumed by Steller sea lions in Alaska in 1998 was 12% of the combined pollock and cod catch (Table 3).

Caution should also be used when making inferences about competition and prey availability even when estimates of prey biomass and catch are size-specific. Spatial and temporal distributions of prey (and fishing) at the local scale determine the availability of food resources for Steller sea lions. Estimates of total prey abundance are not enough to make inferences about the food that is available to Steller sea lions. For example, if estimates of the amount of food that Steller sea lions require were less than the estimated available prey biomass (minus the prey taken by fisheries), it would not necessarily mean that Steller sea lions had enough to eat. Sea lions may not have access to all of the prey due to local differences between their foraging space and time and the spatial and temporal distribution of the fish. Local prey densities encountered by Steller sea lions are more relevant than absolute abundance when assessing prey availability.

Our study provides the first estimates of the biomass of prey consumed by Steller sea lions in different regions of Alaska. However, our estimates of prey consumption are neither species-specific nor size-specific and have considerable uncertainty associated with them. Thus, the management applications of our findings are limited by the quality of data currently available for Steller sea lions. Nevertheless, our estimates of consumption shed light on the trophic relationships between Steller sea lions and their prey and provide insights into possible relationships between food consumption and differential rates of population decline in different regions of Alaska. As more detailed diet information becomes available for Steller sea lions in Alaska, our model can be used to provide more refined estimates of prey consumption that can be incorporated in prey stock assessments and management decisions (e.g. Hollowed et al., 2000).

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Appendix I

Energy density of prey of Steller sea lions in Alaska. Length and energy-density data are ranges, means, or ranges of means depending
BC=bomb calorimetry).

Species	Location	Time of year
Cephalopods		
squid	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
squid (5 spp.)	Gulf of Alaska, Bering Sea, north Pacific Ocean	Feb, Jun, Jul
Flatfish		
arrowtooth flounder	Gulf of Alaska, Bering Sea	Feb, Jul, Aug
English sole	Washington	Jan–Mar, Jun, Jul, Sep–Dec
Pleuronectidae (≥2 spp.)	Gulf of Alaska	May–Sep
yellowfin sole	Gulf of Alaska	Jan–Nov
Forage fish		
capelin	Gulf of Alaska, Bering Sea	Jul, Aug
	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Bering Sea	
	Gulf of Alaska	May–Sep
	Gulf of Alaska, Bering Sea	Feb, Jun–Sep
eulachon	Gulf of Alaska	Mar, Aug
	Gulf of Alaska	May–Sep
	Gulf of Alaska, Bering Sea	Feb, Mar, Jun–Sep
Pacific herring	Gulf of Alaska, Bering Sea	Jul, Aug
	Gulf of Alaska	May–Sep
	Gulf of Alaska	Aug
	Gulf of Alaska	spring, fall
	Gulf of Alaska	Mar, Dec
	Gulf of Alaska, Southeast Alaska, British Columbia	
Pacific sandlance	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Gulf of Alaska	May–Sep
	Gulf of Alaska, Bering Sea	Apr–Sep, Nov

Appendix I

on the data that were available. Method is the technique used to obtain the energy density value (PC=proximate composition analysis,

Age or length (or both)	Energy density (kJ/g wet mass)	Method	Source
7–13 cm	3.81	PC	Van Pelt et al. (1997)
	3.85–6.53	BC	Perez (1994)
	5.15	BC	Perez (1994)
adult, 39–40 cm	4.90 (Mar)	BC	Dygert (1990)
	5.95 (Oct)		
7–15 cm	2.86–3.95	PC	Anthony et al. (2000)
juvenile, 18–21 cm	3.3–3.5 (May)	BC	Paul et al. (1993)
adult, 24–29 cm	4.4 (Jun)		
	7.03	BC	Perez (1994)
age 1, 8–9 cm	4.84 (age 1)	PC	Van Pelt et al. (1997)
age 2, 10–12 cm	3.54–4.67 (age 2)		
	5.50	BC	Miller[1]
age 1, 5–8 cm	4.17 (age 1)	PC	Anthony et al. (2000)
age >1, 8–13 cm	6.7 (age >1, Jun)		
	3.7 (age >1, Sep)		
8–13 cm (Gulf)	5.26 (Gulf)	PC	Payne et al. (1999)
13–15 cm (BS)	6.48 (BS)		
	11.05 (August)	BC	Perez (1994)
	10.96 (March)		
age >0, 14–20 cm	7.49	PC	Anthony et al. (2000)
10–23 cm	10.10 (Feb–Mar)	PC	Payne et al. (1999)
	10.62–10.86 (Jun–Sep)		
	5.44 (BS)	BC	Perez (1994)
	11.72 (Gulf)		
age 0, <10 cm	3.69 (age 0)	PC	Anthony et al. (2000)
age >0, 10–19 cm	5.84 (age >0)		
6 cm	3.43	PC	Payne et al. (1999)
ages 0–7	5.7 (age 0, fall)	BC	Paul et al. (1998a)
	8.0 (age 1, fall)		
	9.4–10.2 (age 2, fall)		
	4.4 (age 0–1, spring)		
	5.2–6.3 (ages ≥2, spring)		
age 0, 8–9 cm	5.2 (Dec)	BC	Paul and Paul (1998)
	3.4–3.8 (Mar)		
	7.95	PC[2]	Stansby (1976)
age 0, 8–9 cm	4.95 (age 1)	PC	Van Pelt et al. (1997)
age 1, 11–13 cm	3.18 (age 0)		
age ≥2, 15–19 cm	5.67 (age ≥2)		
age 0, 7–10 cm	6.5 (age 0, Jun)	PC	Anthony et al. (2000)
age >0, 10–19 cm	4.8 (age 0, Jul)		
	5.3 (age 0, Aug)		
	5.6 (age >0, Jun)		
	4.9 (age >0, Sep)		
7–15 cm	5.20 (Gulf)	PC	Payne et al. (1999)
	6.11 (BS)		

continued

Appendix I (continued)

Species	Location	Time of year
Pacific sandlance (cont.)	Gulf of Alaska	Feb, Jun–Nov
Gadids		
Pacific cod	Gulf of Alaska, Bering Sea	Jul, Aug
	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Gulf of Alaska	May–Sep
	Gulf of Alaska	Mar–May, Jul, Oct–Dec
walleye pollock	Gulf of Alaska, Bering Sea	Mar, Jul, Aug
	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Bering Sea	
	Gulf of Alaska	May–Sep
	Gulf of Alaska	Aug
	Gulf of Alaska	Mar, May, Jun, Aug, Oct
	Gulf of Alaska	Mar–Apr
	Gulf of Alaska	
Hexagrammids		
Atka mackerel	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Gulf of Alaska	Aug
greenling	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
lingcod	Gulf of Alaska	May–Sep
Salmon		
chinook		
coho		
pink	Gulf of Alaska	May–Sep
	Gulf of Alaska	May–Jun
sockeye	Gulf of Alaska	May–Sep
	northeast Pacific Ocean	entire life cycle
	southeast Bering Sea	Jul (prior to river entry)
Other		
pricklebacks	Gulf of Alaska	Jun, Aug
pricklebacks (6 spp.)	Gulf of Alaska	May–Sep
rockfish (*Sebastes* spp.)	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
rockfish (≥3 *Sebastes* spp.)	Gulf of Alaska, Bering Sea	Feb, Jul, Aug
sculpins (4 spp.)	Gulf of Alaska, Bering Sea	Feb, Jul, Aug
sculpins (12 spp.)	Gulf of Alaska	May–Sep

[1] Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Rep. MMC-75/08, 27 p. U.S. Marine Mammal Commission, Washington, D.C.

[2] We assumed lipid = 39.3 kJ/g and protein = 17.8 kJ/g (Anthony et al. 2000).

Appendix I (continued)

Age or length (or both)	Energy density (kJ/g wet mass)	Method	Source
age 0, 6–9 cm age 1 12–14 cm	3.40–3.55 (age 0, 6 cm) 4.62–4.86 (age 0, 9 cm) 3.22–3.32 (age ≥1, Nov) 3.23–3.25 (age ≥1, Feb) 5.46–5.75 (age ≥1, Jun–Jul)	PC	Robards et al. (1999)
	3.93	BC	Perez (1994)
7–10 cm	2.94	PC	Van Pelt et al. (1997)
age 0, 6–9 cm age >0, 11–14 cm	3.65 (age 0) 3.54 (age >0)	PC	Anthony et al. (2000)
56–74 cm	4.00–4.30 (Mar) 3.33–3.38 (Jul) 4.13–4.49 (Dec)	BC	Smith et al. (1990)
43–53 cm	4.64	BC	Perez (1994)
age 0, 5–9 cm	2.73	PC	Van Pelt et al. (1997)
	5.89	BC	Miller[1]
age 0, 5–6 cm age >0, 12–18 cm	3.47 (age 0) 3.24 (age >0)	PC	Anthony et al. (2000)
7–8 cm	3.93	PC	Payne et al. (1999)
3–11 cm	2.7 (Jun) 3.4 (Aug) 3.6 (Oct) 3.4–4.0 (Mar) 4.0 (May)	BC	Paul et al. (1998b)
adult	3.68–4.03 (ripe) 3.26–3.41 (spent)	BC	Smith et al. (1988)
juvenile, <34 cm	5.45	BC	Harris et al. (1986)
7 cm	4.02	PC	Van Pelt et al. (1997)
12 cm	4.66	PC	Payne et al. (1999)
6–7 cm	3.45	PC	Van Pelt et al. (1997)
7–9 cm	3.98	PC	Anthony et al. (2000)
equation relating energy density to weight	6.06 (300 g) 8.72 (3 kg)		Stewart and Ibarra (1991)
equation relating energy density to weight	6.06 (300 g) 8.72 (3 kg)		Stewart and Ibarra (1991)
age 0, 6–10 cm age >0, 10–14 cm	3.41 (age 0) 3.73 (age >0)	PC	Anthony et al. (2000)
fry, 3–6 cm	3.2–4.4	BC	Paul and Willette (1997)
age 0, 7–8 cm	4.35	PC	Anthony et al. (2000)
entire life cycle	6.68 (300 g) 7.77 (2.1 kg)		Brett (1983)
adult, 49 cm	6.89–7.69	PC	Hendry and Berg (1999)
9–24 cm	5.40	PC	Payne et al. (1999)
8–30 cm	4.11–4.90	PC	Anthony et al. (2000)
4–6 cm	2.97	PC	Van Pelt et al. (1997)
	5.77–6.23 5.56 (northern rockfish, BS, Jul) 6.85 (northern rockfish, Gulf, Feb)	BC	Perez (1994)
	3.51–5.19	BC	Perez (1994)
4–22 cm	3.05–5.26	PC	Anthony et al. (2000)

A Monte Carlo demographic analysis of the silky shark (*Carcharhinus falciformis*): implications of gear selectivity

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Demographic analysis has recently been used as a tool to approximate the dynamics of shark populations (Cailliet, 1992; Sminkey and Musick, 1996; Au and Smith, 1997; Cortés, 1999). The widespread use of demographic models for shark species, however, is hampered by a paucity of information on vital rates, which are required as input parameters for the models. A vital rate of special importance is natural mortality, which remains unknown for most shark species and many other marine taxa. Demographic models thus must often rely on indirect methods of natural mortality estimation rather than empirically observed values specific to a given population. Several methods to estimate natural mortality have shown promise for shark demographic analysis (Cortés, 1998). Other vital rates such as fecundity, although often strongly influenced by size and age, likely also vary independently of time over the lifespan of individuals within a population. Incorporation of Monte Carlo simulation in demographic models has been used to account for some of this uncertainty in vital rate estimates and construct confidence intervals for model output (Cortés, 1999; 2002).

One of the most valuable aspects of demographic modeling is the ability to examine how populations might respond to various levels of fishing mortality (Au and Smith, 1997; Cortés, 1998; Smith et al., 1998; Simpfendorfer, 1999). To date, most authors have used empirical estimates of fishing mortality (F) and either applied them uniformly to all age groups or have produced various scenarios with F applied starting at a particular age to simulate various fisheries management schemes (Sminkey and Musick, 1996; Au and Smith, 1997; Liu and Chen, 1999). Gear selectivity and its effect on F at various ages, however, has not been incorporated into demographic models even though it is very likely that some selection occurs. Here, we produce a demographic analysis of the silky shark (*Carcharhinus falciformis*) off the southeastern United States. Monte Carlo methods are used to simulate variability in model input parameters, and multiple scenarios are considered, incorporating natural mortality only, and added fishing mortality components. We include in our analysis scenarios that reflect possible longline gear selectivity for silky sharks, using catch-at-age information estimated from length-frequency data provided by the U.S. pelagic longline observer program for the southeastern U.S. coast. Finally, we compare scenarios that incorporate the same mean value of fishing mortality, but with different assumptions of selectivity patterns. The results of the demographic analysis are discussed in the context of the robustness of model assumptions.

Materials and methods

Life history parameters for the silky shark demography were obtained from the best available literature sources. Von Bertalanffy parameters of L_∞ = 311 cm total length, K = 0.101/yr, and t_0 = –2.718 yr were taken from Bonfil et al. (1993). To account for some of the uncertainty in the estimate of age-at-maturity (t_{mat}) of 12 years given by Bonfil et al. (1993), values for t_{mat} were drawn at random from a discrete probability distribution of P = 0.25, 0.5, and 0.25 for ages 11, 12, and 13, respectively. Longevity (t_{max}) was similarly varied by assigning the estimate of Bonfil et al. (1993) of 22 years a P = 0.5 and linearly decreasing P by 50% for each subsequent year.

Estimates of natural mortality (M) were selected by using three methods: Peterson and Wroblewski (1984), Chen and Watanabe (1989), and Jensen (1996) (Table 1). For the Peterson and Wroblewski method, weights-at-age were determined by calculating total length-at-age from the von Bertalanffy growth function, and then converting these values to fork length and weight (in grams) by using the relationships given by Kohler et al. (1995) for the silky shark. Wet weight was used instead of dry weight to generate values of M. Annual survival (S_x; $S=e^{-M}$, x=age) values were randomly drawn from a distribution in which the three methods of calculating mortality rates had equal probability.

Fecundity (m_x), the number of female pups produced per each year of life, was calculated by combining the data of Fourmanoir (1961), Bane (1966), Gilbert and Schlernitzauer (1966), Branstetter (1987), and Bonfil et al. (1993), which yielded a mean of 10.3 (SD=2.213, n=16) pups per litter. Observations in the literature of litter sizes lower than five pups were not included because of the possibility that females might have aborted pups from one uterus during capture

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Table 1

Natural mortality (M) estimation methods used in demographic models for silky sharks (*Carcharhinus falciformis*). W = body weight in grams, K, t_0 = von Bertalanffy growth parameters, and $t_{\max}$ = maximum age.

Citation	Method
Peterson and Wroblewski (1984)	$M = 1.92\,W^{-0.25}$
Jensen (1996)	$M = 1.6K$
Chen and Watanabe (1989)	$M(t) = K / [1 - e^{-K(t-t_0)}]$, for $t = 0$ through 11
	$M(t, t_{max}) = [1/(t_{max} - t)] \ln [(e^{Kt_{max}} - e^{Kt_0})/(e^{Kt} - e^{Kt_0})]$

(Branstetter, 1987; Bonfil et al., 1993). Pups-per-litter estimates were then converted into female pups per year (m_x) by using the embryo sex ratio of 1:1.17 (male:female) given by Bonfil et al. (1993) and a reproductive cycle of two years suggested by Branstetter (1987). All females were assumed to enter the breeding population after first age-at-maturity, and reproductive senescence was assumed to occur at age ($t_{\max}$+1). Actual values of fecundity (m_x) used as model input were drawn at random from a normal distribution with a mean of 10.3 and a standard deviation of 2.213 calculated as described above, and then scaled to represent female pups per year.

The parameters estimated above were used to construct life tables by using standard methods, but incorporating Monte Carlo simulation for output parameter estimation. Output parameters (net reproductive rate, R_0; mean generation length, G; and intrinsic rate of population increase, r) were calculated by standard demographic methods (Wilson and Bossert, 1971; Krebs, 1985), and r was solved iteratively with the Euler equation.

Various scenarios, each of which varied vital rates as described above, were analyzed. A base scenario incorporated natural mortality only. To attempt to incorporate gear selectivity, we compared a model that incorporated total mortality only (Z, scenario 1) estimated from a traditional catch curve with a model incorporating Z estimated from a modified catch curve method. To produce a catch curve estimate of Z, length-frequency data for silky sharks observed on longlines off the southeastern United States during 1992–98 (NMFS[1]) were used with an age-length key derived from the length-at-age data of Bonfil et al. (1993). The assumptions in this method are that in all years 1) recruitment is constant, 2) fishing mortality is constant, and 3) catchability is equal (there is no gear selectivity). The decrease in population over time is

$$N_t = N_{t-1} e^{-Za},$$

where N_t = population in numbers at time t; and
a = age.

An assumption of gear selectivity was then used to modify the standard catch equation. If one assumes that gear selectivity exists, then Z can no longer be constant and Z can be estimated at each age:

$$-Z = \ln(N_t / N_{t-1}) / a.$$

To avoid positive values of Z at some ages (due to those ages not being present in the catch as predicted by the age-length key) an exponential curve was fitted to the catch-at-age data to produce the values of N_t. Because the value of Z cannot be calculated for age 0 with this method, we assumed that total mortality was the same for ages 0 and 1. The values of Z-at-age produced by this method were used in a demographic model (scenario 2) and compared with scenario 1. For ages where estimates of Z were not reasonable ($Z<M$), the natural mortality estimate was used for that age.

To examine the effect of various patterns of selectivity, we also compared scenarios with the same average value of fishing mortality, but with various assumptions of selectivity patterns. These scenarios added a fishing mortality component into the base scenario. Scenario 3 incorporated the 1997 instantaneous fishing mortality (F) value of 0.093 estimated for Atlantic large coastal sharks (Anonymous[2]) applied uniformly to all age groups. An exponential function of the form $y=be^{(-ax)}$, where $y = F$, x = age, and the mean $F = 0.093$, was fitted to the catch-at-age data assuming zero fishing mortality after age 13 (scenario 4) and a positive level of fishing mortality through all age groups (scenario 5). Scenario 6 applied an F value of 0.034, calculated to produce maximum sustainable yield (MSY) for large coastal sharks (Anonymous[2]), uniformly to all age groups. Scenarios 7 and 8 were constructed in the same manner as scenarios 4 and 5, respectively, but with the mean value of $F = 0.034$.

Each of the scenarios were run 1000 times with vital rates (first age-at-maturity, fecundity, longevity, and natural mortality where appropriate) varying as described above. The 2.5th and 97.5th percentiles of the ranked output were used as approximate percentile confidence intervals for the parameters R_0, G, and r. Finite rates of population increase or decrease (e^r) and approximate percentile confidence intervals were then calculated based on the r value output. All simulations were run by using Microsoft Excel spreadsheet software.

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[1] NMFS (National Marine Fisheries Service). 2000. Unpubl. data. Southeast Fisheries Science Center Pelagic Observer Program, 75 Virginia Beach Drive, Miami, FL 33149.

[2] Anonymous. 1998. Report of the shark evaluation workshop, 109 p. Panama City Laboratory, National Marine Fisheries Service, 3500 Delwood Beach Rd., Panama City, FL 32408.

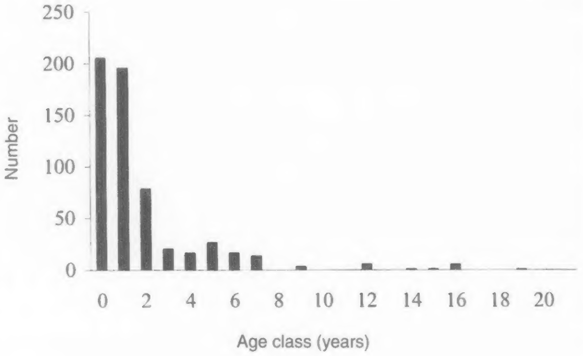

Figure 1

Estimated silky shark (*Carcharhinus falciformis*) catch-at-age from pelagic longlines off the southeastern U.S. coast, 1992–98.

Results

The three methods used to estimate natural mortality yielded annual survivorship (S) values ranging from 0.657 to 0.904 (Table 2). The method of Peterson and Wroblewski produced S values of 0.760 (age 0) to 0.904 (age 22), slightly higher than the values produced by the method of Chen and Watanabe (0.657 to 0.874, ages 0–11; 0.890, ages 12+). The method of Jensen produced the lowest S value (0.851) for ages 7 and above, and the highest survivorship in the first 4 years of life.

The catch-at-age histogram indicated that few silky sharks over the age of 7 years were caught in the southeastern pelagic longline fishery (Fig. 1). The catch curve estimated a Z value of 0.329 (r^2=0.838, Fig. 2). The Z-at-age values calculated from the modified catch curve method predicted values of Z = 0 for ages 12 and above (scenario 2; Table 3). Values of F-at-age used in scenarios 3–8 (Table 3) were as high as 0.287 (scenario 4, age 0).

The results of the base scenario (Table 4) indicated that the silky shark population, in absence of fishing mortality, would increase at a median rate of 4.9 %/yr. The approximate percentile lower confidence limit also showed positive population growth (e^r=1.027). Incorporating the Z obtained from the catch curve into the model (scenario 1) resulted in the greatest rate of population decline of any of the scenarios considered (e^r=0.895). However, the use of the Z-at-age values from the modified catch curve method (scenario 2) produced a positive population increase of 1.8 %/yr.

With estimated F for large coastal sharks in 1997 applied to all age groups (scenario 3), the population would decline at a rate of 4.4 %/yr. Application of exponentially decreasing fishing mortality resulted in a more optimistic median e^r value when the mean F was confined to ages 0–12 (scenario 4), but when mean F was applied to all ages (scenario 5), the output was more pessimistic than that for the constant F = 0.093 model. With F estimated for maximum sustainable yield (scenario 6), the silky shark population would slowly increase at a rate of 1.5 %/yr. Incorporation of variable F-at-age in scenarios 7 and 8 resulted in e^r values slightly higher and lower, respectively, than the constant F scenario.

Table 2

Annual survivorship (S) estimates calculated from three studies based on best available life history information for the silky shark (*Carcharhinus falciformis*).

Age (yr)	Peterson and Wroblewski	Chen and Watanabe	Jensen
0	0.760	0.657	0.851
1	0.799	0.724	0.851
2	0.824	0.766	0.851
3	0.840	0.794	0.851
4	0.853	0.815	0.851
5	0.862	0.830	0.851
6	0.869	0.842	0.851
7	0.875	0.851	0.851
8	0.880	0.858	0.851
9	0.884	0.865	0.851
10	0.887	0.870	0.851
11	0.890	0.874	0.851
12	0.892	0.890	0.851
13	0.894	0.890	0.851
14	0.896	0.890	0.851
15	0.898	0.890	0.851
16	0.899	0.890	0.851
17	0.900	0.890	0.851
18	0.901	0.890	0.851
19	0.902	0.890	0.851
20	0.903	0.890	0.851
21	0.904	0.890	0.851
22	0.904	0.890	0.851

Discussion

The base scenario results given in our study match well those from other demographic models for silky sharks. Using a demographic model that incorporated density-dependence, Smith et al. (1998) found an r value of 0.043 for silky sharks. Cortés (2002) found an average r value of 0.055 for silky sharks from the southern Gulf of Mexico

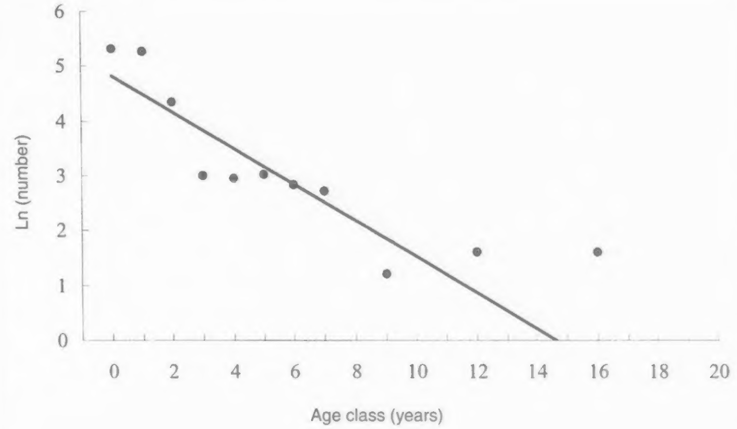

Figure 2

Catch curve for silky sharks (*Carcharhinus falciformis*) from pelagic longlines off the southeastern U.S. coast 1992–98.

using density-independent matrix simulation models. These r values place the silky shark toward the middle of the range of productivity values calculated for a mix of species (Smith et al., 1998; Cortés, 2002).

The pessimistic results of the model that incorporated Z calculated from the catch curve are consistent with the stock assessments that indicate large coastal sharks are overfished and suggest, in particular, that exploitation rates in the pelagic longline fishery may not be sustainable for silky sharks. However, incorporating gear selectivity with the modified catch curve method altered the results, yielding one of the highest rates of population growth of any of the scenarios. If the assumptions about the relationship between the catch curve and selectivity are reasonable, the results indicate that incorporation of gear selectivity into demographic analysis is important.

The importance of considering selectivity as explored by the fishing mortality scenarios was less clear. Scenario 3 indicated that a recently estimated level of fishing mortality would produce declines in the population, whereas scenario 6 indicated that the fishing mortality level producing maximum sustainable yield would result in a slightly increasing population. When exponentially decreasing F-at-age was incorporated (scenarios 4, 5, 7, and 8), the results differed—but much less so than those of scenarios 1 and 2—from those obtained in the constant F scenarios (3 and 6). All the fishing mortality scenarios (3–8) used mean values of F estimated through density-dependent modeling and were used here only as comparative base values.

Stock assessments of northwestern Atlantic shark stocks are based on species groups rather than individual species. These assessments use data from fisheries of various gear types, which may not correctly represent the life history or the pattern of exploitation of an individual species. In that respect, *Carcharhinus falciformis* may be an excellent example. Off the coast of the southeastern United States, pelagic longlines may be the dominant cause of silky shark fishing mortality, whereas bottom longlines rarely capture, and drift gillnets do not capture, this species (Parrack et al., 1993; Trent et al., 1997). Examination of length frequencies from the pelagic longline fishery observer database suggests that age 8+ silky sharks are rarely caught. Therefore, the assumption of constant fishing mortality throughout all age groups for this species is probably invalid, at least for the pelagic fishery off the southeastern United States. If individual species management of silky sharks is ever to become a reality, the patterns of selectivity of longline gear are very important.

It seems logical that the larger the shark, the higher the probability it can bite through the monofilament gangions used by U.S. pelagic longliners and escape. Because size is correlated with age, there must be a functional relationship that describes the probability of retention and capture for a given age. Accurate elucidation of such gear selectivity patterns requires knowledge of the actual size-at-age characteristics of the population that can only be derived from sampling studies in which methods that are not size-selective are used, or that are at least less size-selective than longline gear. These types of comparative data are almost wholly lacking for sharks in the pelagic environment. Indirect methods of estimating selectivity for shark species by comparing catches from gillnets of various mesh sizes have shown promise (Kirkwood and Walker, 1986; Simpfendorfer and Unsworth, 1998). Previous indirect studies of selectivity in hook and line gear (Cortez-Zaragoza et al., 1989; Ralston, 1990) cannot be applied in this case because selectivity in those studies was described as a function of hook size rather than the actual breaking strength of the line, which is the speculated mechanism of selection in the present study. Walker

Table 3

Values of total mortality (Z) or fishing mortality (F) used in demographic models for the silky shark (*Carcharhinus falciformis*). For scenario 1, Z was used instead of estimates of natural mortality (M). In scenario 2, Z was used only when $Z>M$. In scenarios 3–8, F was added to natural mortality.

	Scenario							
	1	2	3	4	5	6	7	8
Age (yr)	Z	Z	F	F	F	F	F	F
0	0.329	0.486	0.093	0.287	0.276	0.034	0.105	0.068
1	0.329	0.486	0.093	0.210	0.225	0.034	0.077	0.058
2	0.329	0.243	0.093	0.164	0.195	0.034	0.060	0.053
3	0.329	0.162	0.093	0.132	0.174	0.034	0.048	0.049
4	0.329	0.121	0.093	0.107	0.158	0.034	0.039	0.046
5	0.329	0.097	0.093	0.087	0.144	0.034	0.032	0.043
6	0.329	0.081	0.093	0.069	0.133	0.034	0.025	0.041
7	0.329	0.069	0.093	0.054	0.123	0.034	0.020	0.040
8	0.329	0.061	0.093	0.041	0.114	0.034	0.015	0.038
9	0.329	0.054	0.093	0.029	0.107	0.034	0.011	0.037
10	0.329	0.049	0.093	0.019	0.100	0.034	0.007	0.035
11	0.329	0.044	0.093	0.009	0.093	0.034	0.003	0.034
12	0.329	0.000	0.093	0.09×10^{-5}	0.087	0.034	0.09×10^{-5}	0.033
13	0.329	0.000	0.093	0.000	0.082	0.034	0.000	0.032
14	0.329	0.000	0.093	0.000	0.077	0.034	0.000	0.031
15	0.329	0.000	0.093	0.000	0.072	0.034	0.000	0.030
16	0.329	0.000	0.093	0.000	0.068	0.034	0.000	0.029
17	0.329	0.000	0.093	0.000	0.063	0.034	0.000	0.029
18	0.329	0.000	0.093	0.000	0.059	0.034	0.000	0.028
19	0.329	0.000	0.093	0.000	0.056	0.034	0.000	0.027
20	0.329	0.000	0.093	0.000	0.052	0.034	0.000	0.026
21	0.329	0.000	0.093	0.000	0.049	0.034	0.000	0.026
22	0.329	0.000	0.093	0.000	0.045	0.034	0.000	0.025
23	0.329	0.000	0.093	0.000	0.042	0.034	0.000	0.025
24	0.329	0.000	0.093	0.000	0.039	0.034	0.000	0.024
25	0.329	0.000	0.093	0.000	0.036	0.034	0.000	0.024
26	0.329	0.000	0.093	0.000	0.034	0.034	0.000	0.023
27	0.329	0.000	0.093	0.000	0.031	0.034	0.000	0.023
28	0.329	0.000	0.093	0.000	0.028	0.034	0.000	0.022
29	0.329	0.000	0.093	0.000	0.026	0.034	0.000	0.022

(1992) incorporated hook selectivity into an age-structured model, but he assumed that all recruited members of a stock had an equal value of catchability with longline gear. We believe that an assumption of equal catchability is incorrect for silky sharks, and sharks in general, hooked on monofilament pelagic longline gear.

Determining actual patterns of selectivity and resulting estimates of fishing mortality-at-age, however, was beyond the scope of our analysis, which was to suggest that patterns of gear selectivity can affect results from demographic models. We chose a simple modification of a traditional catch curve and an intuitive, although arbitrary, assumption of selectivity patterns for silky sharks on pelagic longlines to explore this effect. Arbitrarily derived selectivity schedules were employed previously to examine the potential effects of gear selection in yield-per-recruit models (Goodyear, 1996). Clearly this approach, as applied here, has limitations. For example, the curve fitted to catch-at-age data used to calculate Z values estimated zero total mortality at ages 12+, whereas the catch-at-age data showed a few captures of ages 12+ (Fig. 1). No mortality is assumed for individual animals that escape the gear, although it is possible that some animals may die. Despite shortcomings in the methods to estimate F-at-age values used in our study, better estimates of fishing mortality will require more robust, comparative selectivity data.

Like many other studies of shark populations, the results reported in our study must be considered preliminary

Table 4

Demographic output (R_0=net reproductive rate; G=mean generation length; r=intrinsic rate of population growth; e^r=finite rate of population growth) and lower (LCL) and upper (UCL) approximate confidence limits for the silky shark (*Carcharhinus falciformis*) off the southeastern U.S. coast. The base scenario incorporated natural mortality (M) only; scenario 1 incorporated a constant value of total mortality (Z), scenario 2 incorporated various values of Z-at-age, and scenarios 3–8 incorporated the mean value of fishing mortality (F) shown in the second column.

Scenario	Mean F (or Z)	R_0	LCL	UCL	G	LCL	UCL	r	LCL	UCL	e^r	LCL	UCL
base	none	2.161	1.547	2.959	16.115	14.942	17.570	0.048	0.027	0.071	1.049	1.027	1.074
1	0.329	0.195	0.127	0.284	14.380	13.266	15.484	–0.111	–0.130	–0.091	0.895	0.878	0.913
2	0.065	2.615	2.083	3.158	16.091	14.965	17.582	0.018	0.001	0.032	1.018	1.001	1.033
3	0.093	0.508	0.345	0.724	15.190	14.042	16.544	–0.044	–0.066	–0.022	0.957	0.936	0.978
4	0.093	0.652	0.477	0.886	16.113	14.946	17.546	–0.026	–0.045	–0.008	0.974	0.956	0.992
5	0.093	0.262	0.175	0.375	15.427	14.235	16.857	–0.084	–0.105	–0.066	0.919	0.900	0.936
6	0.034	1.266	0.898	1.747	15.755	14.605	17.176	0.015	–0.006	0.037	1.015	0.994	1.038
7	0.034	1.392	0.991	1.920	16.105	14.937	17.565	0.021	–0.001	0.043	1.021	0.999	1.044
8	0.034	1.130	0.783	1.539	15.815	14.623	17.261	0.008	–0.015	0.029	1.008	0.985	1.029

because of the lack of validated age and growth information and the uncertainty in the estimates of longevity and fecundity for the silky shark. It is difficult to determine how representative the von Bertalanffy parameters (Bonfil et al., 1993), which were derived from silky sharks in the Campeche Bank in the southern Gulf of Mexico, are for silky shark populations from the entire southeastern U.S. Atlantic. Although tagging data (Kohler et al., 1998) indicate movement of silky sharks between the Gulf of Mexico and the U.S. Atlantic coast, the small number of tagged and recaptured individuals makes firm conclusions about whether these are the same or separate stocks very difficult. The age and growth results of Bonfil et al. (1993) from the southern Gulf of Mexico differed from a study on silky sharks by Branstetter (1987) in the northern Gulf. It is possible, however, that these variations may be a result of methodological or sampling differences because Branstetter's (1987) data came from pelagic longline operations and had fewer specimens over 250 cm TL, compared to Bonfil et al.'s (1993) data which came mainly from specimens caught in gillnet fisheries. Even if migration of silky sharks occurs between the northern Gulf of Mexico, southern Gulf of Mexico, and southeastern U.S. Atlantic coastal region, the populations of sharks in these areas might have significant life history differences. Given the absence of age and growth studies from Atlantic silky sharks, the Gulf of Mexico studies must be regarded as the best available age and growth information for this species. Similarly, fecundity and longevity estimates are relatively uncertain. Especially important in fecundity estimates is information regarding age-specific birth rate and the possibility of reproductive senescence, which can affect demographic results.

As with other demographic analyses, theoretical estimates of natural mortality (M) were used in our study. It has been shown that the output of demographic models of shark populations is particularly sensitive to changes in M, especially during the first few years of life (Sminkey and Musick, 1996; Liu and Chen, 1999; Cortés, 2002). Moreover, results may vary considerably in analyses that use different methods of M estimation (Simpfendorfer, 1999). In recognition of these limitations, three different methods were used here to estimate M. The methods of Chen and Watanabe (1989) and Jensen (1996) are based on a relationship between M and growth rates. Because the age and growth information for silky sharks is unvalidated, the von Bertalanffy growth parameters used in our study may not adequately describe individuals from the population analyzed. Finally, the method of Peterson and Wroblewski (1984) involves the assumption that M is due primarily to predation. Although this may be true for the younger ages of large coastal sharks like the silky shark, it may not be true for the larger, older sharks. Additionally, wet weight was used instead of dry weight, as prescribed in the original equation of Peterson and Wroblewski (1984), because the estimates of M obtained by using wet weight seem more believable for sharks (Cortés, 2002). Despite the difficulties associated with all three methods of estimating natural mortality, these methods, together with catch curves and tag-recapture studies, are the only methods available for estimating M. The use of Monte Carlo simulation to randomly vary the estimates of natural mortality can account for some of the uncertainty associated with these methods (Cortés, 1999; 2002).

Conclusions from this analysis of the silky shark population off the southeastern U.S. coast are similar to those for other large shark species. Even under scenarios assuming natural mortality only, the population would grow at a fairly slow rate, and even moderate levels of fishing mortality might produce population declines. Inclusion of age-dependent patterns of fishing mortality into the analyses, however, appear to substantially affect model results. Several key elements that need to be clarified to obtain a more conclusive analysis for silky sharks include validated age and growth information, life history parameters such as longevity, fecundity, and natural mortality, and estimates of age-dependent fishing mortality.

Acknowledgments

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Indirect estimates of natural mortality rate for arrowtooth flounder (*Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*)

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Indirect estimates of instantaneous natural mortality rate (M) are widely used in stock assessment and fisheries management. They are essentially a form of meta-analysis, in which prior information on M and key life history parameters from a variety of stocks is used to estimate M for the stock in question.

In this study we report indirect estimates of M for arrowtooth flounder (*Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*) obtained by the methods described in Gunderson (1997), and a modification of Pauly's method (1980), and compare them with estimates previously derived by Hoenig's (1983) method. Pauly's original method was based on the correlation of M with von Bertalanffy growth parameters (K and L_∞) and temperature. The modification we used was indicated by a number of reviews of Pauly's data (Charnov, 1993; Pascual and Iribarne, 1993; Jensen, 1996) and relies only on the correlation between M and K. The high correlation between these variables has been observed in a number of taxa and is the basis for the M–K "invariant" used widely in life history theory (Beverton, 1992; Charnov, 1993).

Gunderson's method is based on the high correlation between reproductive effort and natural mortality rate and has a well-established basis in experimental ecology and life history theory (Reznick, 1996). Increases in reproductive effort often come at a cost, and trade-offs between reproductive effort and adult growth or survival have been reported in a wide range of field studies and manipulation experiments (Roff, 1992; Stearns, 1992). Gunderson (1997) found a linear relationship (r^2=0.75) between M and reproductive effort as measured by the gonadosomatic index (GSI=ovary weight/somatic body weight) for 28 stocks of fish, and theoretical analysis (Charnov et al., 2001; Charnov, 2002) has shown that this equation can be a predictable result when maximizing the lifetime production of young.

Pascual and Iribarne (1993) noted that one shortcoming of indirect methods of estimating natural mortality is that no variance estimate is usually associated with the predicted value of M. In this study, we used the delta method (Seber, 1982) to derive estimates of the variance of predicted values of M using Gunderson's technique and Jensen's (1996) modification of Pauly's technique. In the case of the method developed by Hoenig, where natural mortality is estimated from longevity, no comparable variance estimator could be obtained because the results depend on the sample size used to estimate longevity (Hoenig, 1983).

Materials and methods

Data on darkblotched rockfish were collected in 1986 and 1987 during research surveys conducted off the Oregon coast (43°10′–45°50′) aboard commercial groundfish and shrimp trawlers. Fish were weighed to the nearest gram, and fork length was measured to the nearest millimeter. Gonads were removed and weighed to the nearest 0.01 g. Gonad color, size, and structure were recorded for each specimen, and macroscopic observations were made at sea for the presence of fertilized eggs, eyed larvae, and residual larvae in the ovaries. Gonads were preserved in 10% phosphate-buffered formalin and histological analysis was conducted later in the laboratory for selected specimens. It was assumed that the ovaries collected during November–January were fully mature because oocyte fertilization occurs during December–February (Nichol, 1990). Only mature females (36.7 cm or greater) classified as being in the "vitellogenesis" stage (Nichol and Pikitch, 1994) during November–January (n=28) were used to estimate the parameters for the length–ovary-weight relationship, and fish collected during August–November were added when estimating the length–somatic-weight relationship (total n=86).

Data on arrowtooth flounder were collected from research trawls made during September 1993 on Portlock Bank near the eastern end of Kodiak Island, Alaska (Zimmermann, 1997). Fish (less stomach contents) were weighed (+/–2 g) and fork length (cm)

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Fish. Bull. 101:175–182 (2003).

was obtained. Gonads were assigned a macroscopic maturity stage based on external appearance, and were removed and preserved in 10% formalin buffered with sodium acetate. Gonads were subsequently removed from formalin, weighed (+/–0.001 g) in the laboratory, and classified histologically to maturity stage. Only mature females (47 cm and greater) with ovaries in the "migratory nucleus" stage (Zimmermann, 1997) were used in estimating the length–ovary-weight relation ($n=19$), and fish in the "late vitellogenesis" stage were added when estimating the length–somatic-weight relation (total $n=59$).

A fresh-weight to formalin-weight conversion equation for gonads was obtained by collecting 22 females during a research cruise conducted during late October and early November 1999 off Oregon and northern California. Gonads for these specimens were weighed fresh at sea (+/–2 g) and again after being stored for 1–4 months in 10% formalin buffered with sodium bicarbonate (+/–0.001 g). Fresh ovary weights for these specimens ranged from 2 to 500 g. The equation for conversion of fresh weight to formalin weight obtained by linear regression was

$$\textit{Fresh weight} = 1.04305\,(\textit{formalin weight}) + 1.82277 \qquad (P<0.001)$$

and was used to correct all arrowtooth flounder ovary weights to fresh weights.

The length–somatic-weight (where somatic weight=total weight minus gonad weight) and length–ovary-weight relationships for both species followed allometric ($y=aX^b$) relationships and were fitted by using nonlinear regression (EXCEL SOLVER, Microsoft Corp., 1998). The relation of length to GSI (gonadosomatic index=ovary weight/somatic weight) was fitted to an allometric relationship because the ratio of two allometric relationships will also be an allometric relationship. The length-GSI relationship was then used to predict the GSI for a mature female of average size in the population.

The average size of a mature darkblotched rockfish was estimated to be 42.7 cm, based on the size composition of females greater than 36.5 cm (the size at 50% maturity, Nichol and Pikitch, 1994) during the 1977 NMFS trienniel trawl survey (Rogers[1]). There is no directed fishery for arrrowtooth flounder, and they have been exploited only lightly. As a result, the average size of a mature (47 cm or greater; Zimmermann, 1997) arrowtooth flounder was estimated to be 55.5 cm, based on the size composition in the 1999 NMFS trawl survey, which covered their entire size range with a single gear type (Brown[2]).

The instantaneous rate of natural mortality was estimated from the equation $M=1.79$ GSI developed by Gunderson (1997). The variance of this estimate was estimated using the delta method to obtain

$$\mathrm{Var}(\hat{M}) = \mathrm{Var}(\hat{k}\,GS\hat{I}) = (GS\hat{I})^2\,\mathrm{Var}(\hat{k}) + \hat{k}^2\,\mathrm{Var}(GS\hat{I}),$$

$$\mathrm{Var}(GS\hat{I}) = \left[ef(\overline{L}_m)^{f-1}\right]^2 \mathrm{Var}(\overline{L}_m) + (\overline{L}_m^{2f})\mathrm{Var}(e)$$

$$+\left[e\overline{L}_m^f \ln(\overline{L}_m)\right]^2 \mathrm{Var}(f) + (2\overline{L}_m^f)\left[e\overline{L}_m^f \ln(\overline{L}_m)\,\mathrm{Cov}(e,f)\right];$$

$$\mathrm{Var}(\hat{k}) = \frac{s^2}{\sum (GSI_i - \overline{GSI})^2} \quad \text{(Draper and Smith, 1981)} = 0.03389)$$

where L_m = mean length of a mature female in the unexploited population;

e,f = coefficients in the length-GSI relationship ($\mathrm{GSI}=eL^f$);

s^2 = residual mean square from GSI-M regression equation (Gunderson, 1997);

$GS\hat{I}$ = mean value of GSI used to predict M in this study;

$\overline{GSI}$ = mean value of GSI in regression sample (Gunderson, 1997);

GSI_i = GSI value for i^{th} species in the regression sample; and

$\hat{k}$ = constant from the GSI-M regression = 1.79.

The Var (e), Var (f), and Cov (e,f) terms in Var ($GS\hat{I}$) were estimated from the variance-covariance matrix of a nonlinear regression algorithm for the length-GSI relationship by using S-PLUS (Venables and Ripley, 1997). The Var($\overline{L}_m$) term was estimated from the length-frequency data used to estimate $\overline{L}_m$.

Indirect estimates of M were also obtained using a modification of Pauly's (1980) method. Jensen (1996) showed that in terms of either the standard error or proportion of variation in predicted M, the simple linear regression of M on the von Bertalanffy growth parameter K is as good as a multiple linear regression model that includes asymptotic size and temperature. The correlation between M and K is a predictable result from life history theory when optimizing the trade-off between survival and fecundity (Jensen, 1996), and has been shown to occur in a wide variety of invertebrate and vertebrate groups (Beverton, 1992; Charnov, 1993).

Pauly's (1980) data for 175 stocks of fish were used to estimate the coefficient ($\hat{g}=1.598$; $r^2=0.72$) in the equation $M=\hat{g}K$. Estimates of K were obtained by fitting age-length data (sexes combined) for 3930 darkblotched rockfish and 706 arrowtooth flounder to the Von Bertalanffy growth model (Ricker, 1975) by using a nonlinear regression algorithm in AD Model Builder (Fornier, 2001; Wilderbuer[3]). The variance of the estimates was estimated with the delta method to be

$$\mathrm{Var}(M) = \hat{g}^2\mathrm{Var}(K) + K^2\mathrm{Var}(\hat{g}).$$

The Var(K) term was estimated by using AD Model Builder, and Var($\hat{g}$) was estimated by using Pauly's data, and the same method used above to estimate Var($\hat{k}$) (Draper and Smith, 1981).

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[1] Rogers, J. B. 2001. Personal commun. Northwest Fisheries Science Center, 2030 SE Marine Science Dr., Newport OR 97365.

[2] Brown, E. S. 2002. Personal commun. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

[3] Wilderbuer, T. K. 2002. Personal commun. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

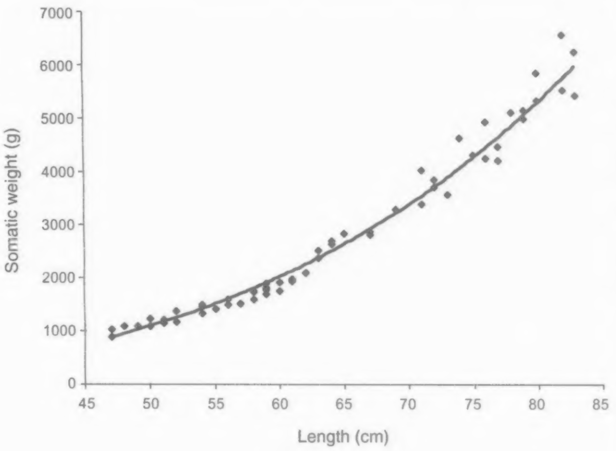

Figure 1

Length–somatic-weight relationship for arrowtooth flounder (*Atheresthes stomias*).

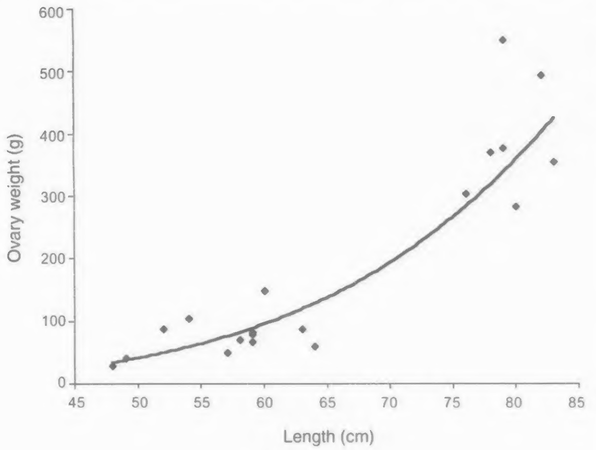

Figure 2

Length–ovary-weight relationship for arrowtooth flounder (*Atheresthes stomias*).

Results

The length–somatic-weight and length–ovary-weight data for arrowtooth flounder (Figs. 1 and 2) and darkblotched rockfish (Figs. 3 and 4) both conformed to allometric relationships. Length–somatic-weight data for both species conformed closely to the model fitted to them (r^2=0.90–0.98, Table 1). The data for the length–ovary-weight relationship conformed to the fitted line reasonably well for arrowtooth flounder (r^2=0.85) and only moderately well for darkblotched rockfish (r^2=0.65). Although sample sizes for ovary weight data were low for both species (n=19–28), the histological classifications available for arrowtooth flounder helped to assure that all fish collected were fully mature and to minimize the scatter about the length–ovary-weight relationship. The scatter about the length-GSI relationships for both species (Figs. 5 and 6) was relatively high (r^2=0.32 for arrowtooth and 0.36 for darkblotched rockfish). The GSI estimates for both species were at the lower end of the distribution of the GSI and *M* values used to develop the original predictive relationship (Fig. 7).

Indirect estimates of the instantaneous rate of natural mortality were estimated to be $M = 0.08$ for arrowtooth flounder with the gonadosomatic index and 0.11 with the growth coefficient *K* (Table 1). Corresponding estimates for darkblotched rockfish differed more substantially (M=0.11 with the gonadosomatic index and 0.30 with *K*). Precision for the estimates of *M* was higher for the estimates based on *K* (CV=5 to 12%) than for those based on the gonadosomatic index (CV=17%).

Table 1

Estimates of instantaneous natural mortality rate (*M*) using the gonadosomatic index (GSI), von Bertalanffy growth coefficient (*K*), and maximum age. Allometric coefficients are shown for length–ovary-weight ($y=aL^b$), length–somatic-weight ($y=cL^d$), and length-GSI ($y=eL^f$) relationships. CI = approximate 95% confidence interval.

	Arrowtooth flounder	Darkblotched rockfish
Mean length (cm)	55.5	42.7
a	0.000000591	1.33E-09
b	4.62	6.57
r^2	0.85	0.65
n	19	28
c	0.0022	0.0322
d	3.35	2.82
r^2	0.98	0.90
n	59	86
e	0.000422	0.00000154
f	1.16	2.82
r^2	0.32	0.36
n	19	28
GSI	0.045	0.0598
VAR (GSI)	0.0000344	0.0000705
M (Gunderson)	0.081	0.107
VAR (*M*)	0.00018	0.00035
SE (*M*)	0.0134	0.0186
CI	0.054–0.108	0.07–0.144
K	0.0701	0.1852
Var (*K*)	0.000060	0.0000085
M (Jensen)	0.112	0.296
Var (*M*)	0.000175	0.000175
SE (*M*)	0.0132	0.0132
CI	0.09–0.14	0.27–0.32
Max. age (yr)	23	105
M (Hoenig)	0.18	0.05

Discussion

An estimate of Z=0.18 was previously obtained for arrowtooth flounder by using Hoenig's (1983) relationship between total instantaneous mortality rate (Z) and maximum age in 84 stocks of fish, and an estimated maximum age of 23 years (Turnock et al.[4]). Because this stock has been exploited only lightly, it was assumed that the resulting estimate of Z was equivalent to M. The resulting estimate was somewhat higher than the value obtained from reproductive effort (M=0.08) or K (M=0.11) and outside the approximate 95% confidence limits (±2SE) for both estimates (Table 1).

A range of maximum ages (60 to 105 years) was previously used to obtain estimates of Z (assumed to be approximately equal to M) = 0.025–0.05 for darkblotched rockfish based on Hoenig's method, due to uncertainties in age determination (Rogers et al.[5]). An estimate of M=0.05 provided the best fit to a population dynamics model, although it is somewhat lower than the estimate of M=0.11 obtained in this study with the gonadosomatic index and substantially lower than the estimate of M=0.30 with the growth coefficient K. The estimate obtained with Hoenig's method was once again outside the approximate 95% confidence limits for the other indirect estimates.

Although none of the data on somatic and ovary weights were collected with the specific aim of estimating natural mortality, they served to provide a reasonable estimate of *M* for arrowtooth flounder and a first approximation of this parameter for darkblotched rockfish. More detailed histological data on the ovaries used in the darkblotched rockfish analysis would have improved the reliability of this estimate and a larger sample size of mature ovaries for both species would have been preferable.

The estimates of *M* derived from the growth coefficient *K* (Table 1) were obtained by using age-length data for sexes combined because most of the original data (Pauly, 1980) was in this format. However, because of sexual dimorphism in growth, estimates of *M* would have differed if males and females had been treated as separate "stocks" as was done for 33 of the observations in Pauly's database. Sexual dimorphism was substantial for arrowtooth flounder, where K was 0.194 (corresponding to an estimated M=0.31) for males and 0.065 (M=0.10) for females and was less pronounced in darkblotched rockfish, where K was 0.211 (M=0.34) for males and 0.164 (M=0.26) for females. Averaging these sex-specific estimates would not change

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[4] Turnock, B. J., T. K. Wilderbuer, and E. S. Brown. 1999. Arrowtooth flounder. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 226–253. North Pacific Fishery Management Council, Anchorage, AK.

[5] Rogers, J. B., R. D. Methot, T. L. Builder, K. Piner, and M. Wilkins. 2000. Status of the darkblotched rockfish (*Sebastes crameri*) resource in 2000. *In* Stock assessment and fishery evaluation: appendix to the status of the Pacific Coast groundfish fishery through 2000 and recommended acceptable biological catches for 2001, 71 p. Pacific Fishery Management Council, Portland, OR.

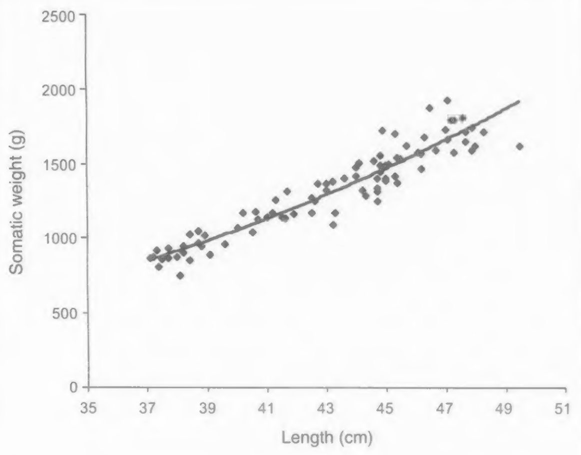

Figure 3

Length–somatic-weight relationship for darkblotched rockfish (*Sebastes crameri*).

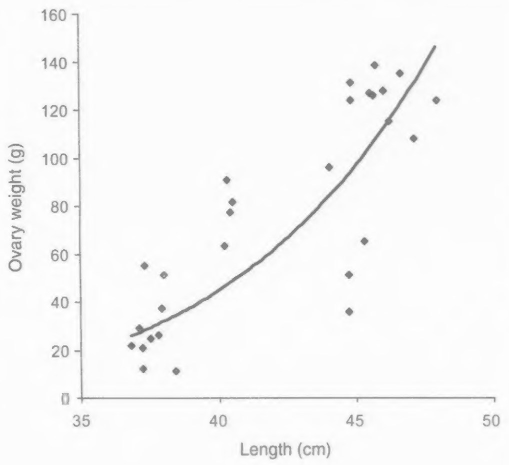

Figure 4

Length–ovary-weight relationship for darkblotched rockfish (*Sebastes crameri*).

the darkblotched estimate of M appreciably from what was obtained by pooling the age-length data to estimate a common K, but the estimate for arrowtooth flounder would increase from 0.11 to 0.21.

All indirect methods of estimating M rely on the correlation established in their basic data set (28 fish stocks for Gunderson, 175 for Pauly, and 84 for Hoenig). As a result these methods are subject to bias in the estimates of M, K, maximum age, and reproductive effort in the original correlation data, and in the estimates of these parameters being used to extrapolate the correlations to new species. Although Pauly's database is the most extensive (in terms of the number of stocks available), age determination and stock assessment methods have improved in the years since it was initially compiled, and estimates of M have tended to decline. An updated database would probably reduce the estimates of M based on K.

The estimate of maximum age required by Hoenig's method assumes that the age determination technique being employed is unbiased. Validating this assumption is of-

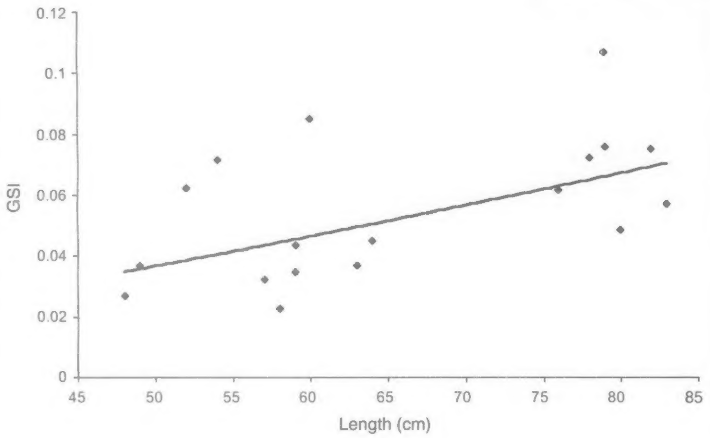

Figure 5
Length-gonadosomatic index (GSI) relationship for arrowtooth flounder (*Atheresthes stomias*).

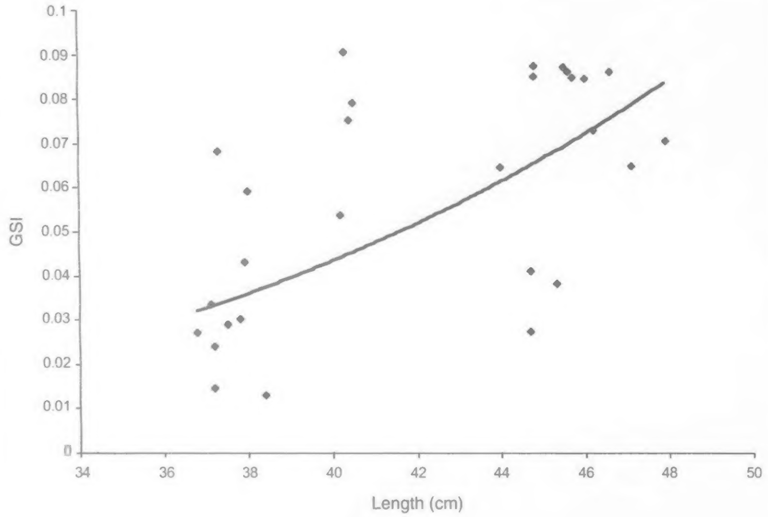

Figure 6
Length-gonadosomatic index (GSI) relationship for darkblotched rockfish (*Sebastes crameri*).

ten difficult for the older, more difficult-to-age individuals but can be accomplished by using a variety of techniques ranging from marking to analysis of radioactive isotopes (Lai et al., 1996). The estimate of longevity is also dependent on sample size and previous fishing history. Hoenig (1983) showed that maximum age tends to increase slowly with increasing sample size after about 200 individuals have been examined, but longevity has probably declined from historical levels because of fishing, particularly in the case of the darkblotched rockfish. A small sample size for age determination, underaging, and previous exploitation would all result in an overestimate of M with Hoenig's method and might explain some of the difference between the estimate of arrowtooth flounder mortality based on reproductive effort or K (M=0.08–0.11) and the previous estimate (M=0.18).

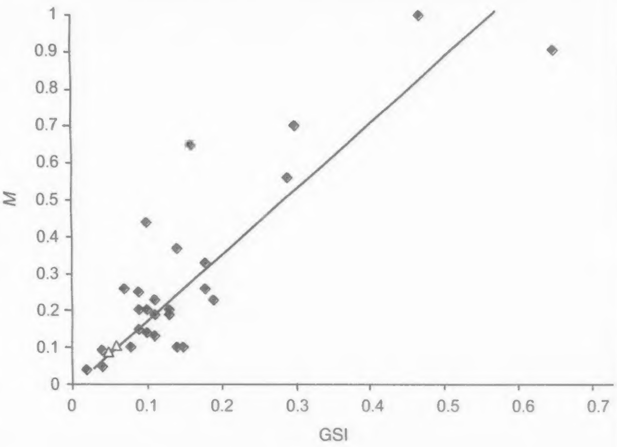

Figure 7

Location of arrowtooth flounder *Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*) (open triangles) in relation to the data set for gonadosomatic index (GSI) and natural mortality rate (M) used to obtain the predictive relation between them (Gunderson, 1997).

In the case of darkblotched rockfish, the estimate of mortality based on reproductive effort (M=0.11) was actually higher than the estimate based on longevity (M=0.05), and neither undersampling nor underaging would explain the differences. Overestimation of the gonadosomatic index (and the estimated M) by using macroscopic rather than histological criteria to classify maturation stage may explain the higher estimate but seems less likely than underestimating it because several oocyte size classes that might be included in the "vitellogenesis" stage are not fully developed. Underestimation of the mean length of a mature female could also lead to an estimate of GSI (and M) that is too low, but estimates of GSI are relatively insensitive to length. For darkblotched rockfish, the mean length of a mature female would have to be 32.4 cm (below the size at maturity) in order for M to equal 0.05.

Indirect estimates of M offer access to a meta-analysis that can be used to explore consistency of natural mortality estimates with prior knowledge on a variety of stocks and put these estimates in the broader context of life history theory. The use of several alternative indirect techniques can minimize bias in stock assessment and expose any misconceptions or errors regarding reproductive biology or age determination at an early stage in a stock assessment program.

Bias is clearly a more important problem than precision when using indirect methods to estimate M. Each of the methods used in our study has a firm basis in life history theory (the M–K and M–GSI "invariants") or population dynamics ($Z \approx 1$/maximum age), and when derived from a database for a large number of species, they can be relatively precise (CV=5–17% for the estimates made in this paper). Nevertheless, many of the original data points on which these relationships are based have become outdated as improved methods of age determination and stock assessment have come into wide usage and ignoring these outdated data points can lead to significant bias when using them to estimate M. Indirect methods are widely used, and it is important that the databases from which they are derived be continually updated and expanded as new information becomes available.

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Use of parasites in stock identification of the deepwater redfish (*Sebastes mentella*) in the Northwest Atlantic

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An important aspect of fisheries management is the correct delineation of boundaries between fish stocks. With the recent collapse of the groundfish fishery in eastern Canada, redfish (*Sebastes* spp.) has become an increasingly important resource. Currently, the two most economically important redfish species (*S. fasciatus* and *S. mentella*) are partitioned into eight management areas in the Northwest Atlantic (Fig. 1). In this study, we examined the parasite fauna of the deepwater redfish *S. mentella*, collected from different areas in the Northwest Atlantic, to determine if the distribution and abundance of the parasite fauna can aid in stock discrimination of this species and focused on differentiating fish from the Gulf of St. Lawrence (unit 1) from those from the Cabot Strait and Laurentian Channel (unit 2). The deepwater redfish is the most common redfish species in the Gulf of St. Lawrence and is considered to have a more northerly range and deeper distribution than its congeners (Atkinson, 1987; Scott and Scott, 1988).

In eastern Canada, parasites have been successfully employed to discriminate among stocks of another deepwater fish, the Greenland halibut (*Reinhardtius hippoglossoides*) (Arthur and Albert, 1993), as well as Atlantic cod (*Gadus morhua*) (McClelland and Marcogliese, 1994). Moles et al. (1998) suggested that parasites could be used to discriminate among stocks of rockfishes (*Sebastes* spp.) in the Gulf of Alaska, and Stanley et al. (1992) used the monogenean *Microcotyle sebastis* to confirm that the yellowtail rockfish *Sebastes flavidus* was distributed in discrete groups along the Pacific coast of North America. However, there is not much information on *Sebastes* spp. from the Northwest Atlantic because studies of redfish parasites prior to that of Bourgeois and Ni (1984) must be treated with caution because of the possible confusion in identification of redfish species (Moran et al., 1996).

Materials and methods

Host and parasite collections

A total of 170 deepwater redfish of size >22 cm were sampled by bottom trawl from five areas representing four management units off the Atlantic coast of Canada between August 1996 and January 1997. Summer and winter samples were available only in unit 2 (Fig. 1, Table 1). Fish were measured on board, individually bagged, and deep frozen immediately after capture for later examination. Because fish from southwestern Labrador Sea and Flemish Cap were not measured on board, estimates of fresh length were made for these fish by using a regression of fresh length on frozen length obtained from the other fishes.

Fish were thawed in the laboratory, measured (total length), and weighed. Prior to parasitological examination, species of redfish were identified by the number of soft anal-fin rays. Only those that had 8 or more soft rays at the anal fin were retained for the analyses (Ni, 1981). Examinations for metazoan parasites were performed with a stereomicroscope using standard parasitological methods. The external surface was examined and scars from previous infestations of *S. lumpi* were noted. The gills were removed, rinsed, and their arches were detached and examined separately. Because of the pressure changes when redfish were hauled out from the deep water most of the stomachs were everted. The internal organs (heart, liver, spleen, gall bladder, swim bladder, digestive tract, gonads, kidney, urinary bladder) were inspected for parasites (lying free or encapsulated on the exterior),

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Fish. Bull. 101:183–188 (2003).

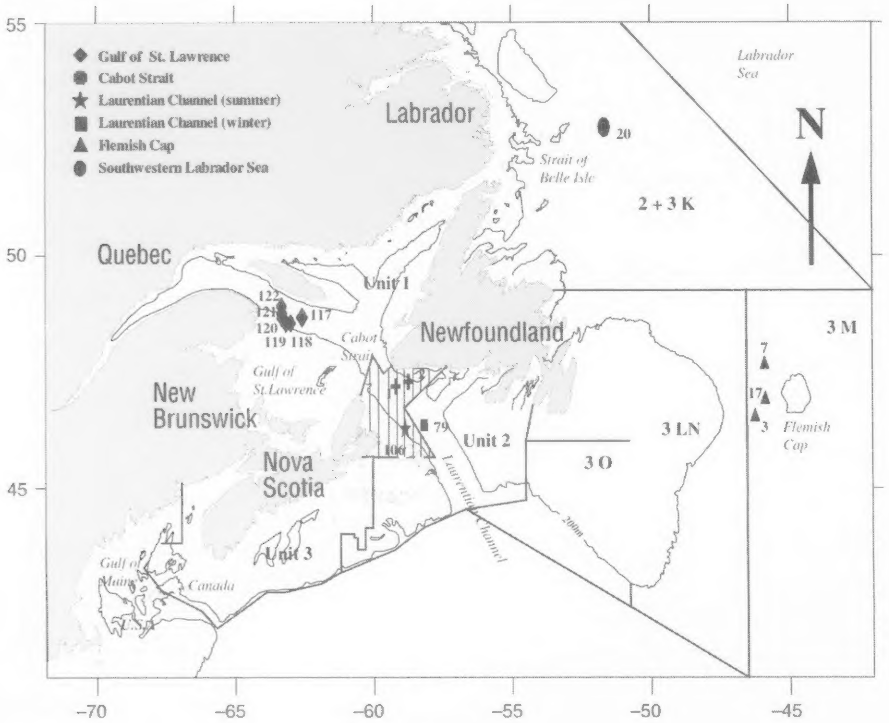
55
50
45
−70
−65
−60
−55
−50
−45
◆ Gulf of St. Lawrence
● Cabot Strait
★ Laurentian Channel (summer)
■ Laurentian Channel (winter)
▲ Flemish Cap
● Southwestern Labrador Sea
Labrador
Labrador Sea
N
20
Strait of Belle Isle
2 + 3 K
Quebec
Unit 1
122
121
120
119 118
117
Cabot Strait
Newfoundland
3 M
7
17
3
Flemish Cap
Gulf of St. Lawrence
New Brunswick
Nova Scotia
79
106
Unit 2
3 LN
3 O
Laurentian Channel
200m
Unit 3
Gulf of Maine
Canada
U.S.

Figure 1

Map of redfish (*Sebastes mentella*) collection sites (various symbols) in the northwestern Atlantic Ocean in 1996 and 1997. The eight areas currently used for redfish management are delineated: 1) subarea 2 and division 3K (southwestern Labrador Sea), 2) divisions 3LN (northern and western Grand Banks); 3) division 3M (Flemish Cap); 4) division 3O (southwestern Grand Banks); 5) unit 1 (Gulf of St. Lawrence); 6) unit 2 (Laurentian Channel); 7) unit 3 (Scotian Shelf); and 8) the Gulf of Maine. The hatched area (Cabot Strait) is part of unit 1 from January to May and unit 2 from June to December. Numbers near collection sites represent set numbers. Jagged line indicates the 200-m depth contour.

separated, and then examined individually. The stomach, pyloric ceaca, and intestine were separated, opened longitudinally, and their contents rinsed into beakers where they were mixed with sodium bicarbonate and allowed to settle to remove endoparasitic helminths. The wall of the stomach, pyloric ceaca, and intestine, and the liver, spleen, kidney, and heart were compressed between glass plates and examined for parasites. The body musculature was removed from the vertebral column, the skin was removed from the fillets, and flaps were thinly sliced and all were inspected for helminths and dead neck stalks or sores caused by old infestations by *Sphyrion lumpi*.

All parasites were sorted into major taxonomic groups, cleaned, and counted for each organ. Nematoda and Copepoda were identified fresh to the lowest taxon and then fixed in 70% ethanol with 10% glycerin. Old cephalothoraces and sores caused by *Sphyrion lumpi* were identified and counted. Digenea and Cestoda were fixed in alcohol-formalin-acetic acid (AFA) and stained in acetocarmine for later identification.

Statistical analyses

Results of analyses may be influenced by variations in factors such as size and sex. In our study, there were no significant differences in mean size of fish sampled from the various regions (Table 1). Males were smaller than females from all regions, except those from the Labrador Sea, where the size difference was reversed. However, none of the parasites retained for multiple parametric analyses differed between the sexes (ANOVA, $P>0.05$).

Because parasite counts for all areas were not normally distributed and normality could not be reached by using various transformations, multiple nonparametric analyses (SAS version 8.0, SAS Institute, Inc., 1999) were used to investigate the usefulness of parasites in discriminating host collections. All parasites used in this analysis were relatively long lived and thus accumulated with host age (length). However, the relationship between size and intensity of certain parasites (*Anisakis simplex*) was not linear, thus rendering covariant analyses inappropriate.

Table 1

Summary of collection data for redfish (*Sebastes mentella*) in the Northwest Atlantic Ocean, 1996–97.

Geographic region	NAFO management area	Latitude-longitude	Date	Number of fish	Mean length (mm) ±SD (range)
Gulf of St. Lawrence	unit 1 (4T)	48.91°N, 63.29°W to 48.66°N, 62.55°W	August 1966	30	330.0±37.4 (220–400)
Cabot Strait	unit 2 (3Pn)	47.19°N, 59.18°W to 47.26°N, 58.72°W	August 1996	49	318.0 ±30.5 (220–390)
Laurentian Channel	unit 2 (4Vn)	46.28°N, 58.84°W	August 1996	31	315.2 ±22.3 (250–350)
Southwestern Labrador Sea	2J	52.74°N, 51.65°W	Autumn 1996	13	321.5 ±59.6 (250–440)
Flemish Cap	3M	47.64°N, 45.89°W to 48.08°N, 44.55°W	Autumn 1996	16	317.0 ±53.6 (228–443)
Laurentian Channel	unit 2 (3Ps)	46.36°N, 58.15°W	January 1997	31	324.5 ±27.5 (260–390)

Table 2

Number of fish involved in redfish (*Sebastes mentella*) statistical comparisons of parasite mean abundance between management units. Winter and summer samples from unit 2 were pooled for these analyses.

	Length class (mm)														
Comparison	220	260	280	290	300	310	320	330	340	350	360	380	390	440	All
FlemishCap—Labrador Sea		2	2	2	2	3	3		3		3			2	22
Flemish Cap—unit 2		3	7	5	12	24	25		14		4	4			98
Labrador Sea—unit 1				2	3		8	5	4		5				27
unit 1 and unit 2	2			5	13		30	18	15	10	6		3		102

The following analyses were performed. For each pair of geographically adjacent management units, that is, across the four stock boundaries encountered around Newfoundland (See Fig. 1), fish were divided into 1-cm length classes. For a given comparison, only length classes containing fish from both units involved were retained. Within each class, the parasite infection intensities were attributed standard normal ranks. The ranks from all length classes were then combined to perform a *t*-test. This test corrects for the effects of host size on parasite mean abundance and for variance heterogeneity while preventing outlying observations from having too much influence. The multiplicity of the statistical tests (many pairs of stocks multiplied by many parasites) was accounted for by a bootstrap procedure (PROC MULTTEST, SAS, version 8, SAS Institute, Inc., 1999). The numbers of fish from each length class involved in the comparisons are detailed in Table 2.

Intensity refers to the number of parasites of a given species in an infected individual fish and mean intensity refers to the mean number of parasites of a given species per infected fish in a sample. Mean abundance is defined as the mean number of parasites of a given species per host, infected and uninfected, in a sample. Prevalence is the proportion of fish infected with a given parasite in a sample, expressed as a percentage (Bush et al., 1997).

Results

Sixteen taxa were found to infect *S. mentella* in eastern Canada in this survey. These included one myxozoan (*Ceratomyxa* sp.), eight digeneans (*Anomalotrema koiae*, *Derogenes varicus*, *Hemiuris levinseni*, *Lecithaster gibbosus*, *Lecithophyllum botryophorum*, *Olssonium turneri*, *Podocotyle reflexa*, and *Progonus muelleri*), two cestodes (*Bothriocephalus scorpii*, and *Scolex pleuronectis* plerocercoids), three nematodes (*Anisakis simplex*, Contracaecinea, and *Hysterothylacium aduncum*), and two copepods (*Chondracanthus nodosus* and *Sphyrion lumpi*). This is the first report of *O. turneri* and *P. muelleri* from *Sebastes* spp.

Preliminary analyses demonstrated that only larvae of *Anisakis simplex* and *Hysterothylacium aduncum*, both anisakid nematodes occurring on the viscera of fish, and the copepod ectoparasite *Sphyrion lumpi* could be used

Table 3

Prevalence (%), mean intensity (no. of parasites, ±SD), and range of intensity of infections of redfish (*Sebastes mentella*) with parasites used as biological tags in the Northwest Atlantic. *n* = sample size.

Region	*n*	Parasite	Prevalence (%)	Intensity (mean ±SD)	Range of intensity
Gulf of St. Lawrence (unit 1-4T)	30	*Anisakis simplex*	53.3	2.8 ±3.1	1–13
		Hysterothylacium aduncum	20.0	1.2 ±0.4	1–2
		Sphyrion lumpi	23.3	1.7 ±0.8	1–3
Cabot Strait (unit 2-3Pn)	49	*Anisakis simplex*	26.5	2.0±1.2	1–4
		Hysterothylacium aduncum	44.9	1.6 ±0.7	1–3
		Sphyrion lumpi	51.0	1.9 ±1.4	1–7
Laurentian Channel–summer (unit 2–4Vn)	31	*Anisakis simplex*	16.1	1.0 ±0.0	1
		Hysterothylacium aduncum	32.3	1.5 ±1.0	1–4
		Sphyrion lumpi	67.7	1.7 ±0.9	1–4
Laurentian Channel–winter (unit 2–3Ps)	31	*Anisakis simplex*	29.0	1.1±0.3	1–2
		Hysterothylacium aduncum	29.0	1.4 ±0.7	1–3
		Sphyrion lumpi	41.9	2.2 ±2.2	1–9
Labrador Sea (2J)	13	*Anisakis simplex*	46.2	25.2 ±35.5	1–92
		Hysterothylacium aduncum	30.8	7.0 ±6.8	2–17
		Sphyrion lumpi	7.7	2.0	2
Flemish Cap (3M)	16	*Anisakis simplex*	56.3	2.7 ±3.5	1–12
		Hysterothylacium aduncum	93.8	93.8 ±92.4	1–259
		Sphyrion lumpi	6.3	10.0	10

to discriminate among redfish stocks (SAS GLM procedure, SAS, 2001). Gastrointestinal digeneans were not used because differences were not noted among regions (SAS GLM procedure). Furthermore, evagination of most of the redfish stomachs during collection caused losses of gastrointestinal parasites and rendered the worm counts unreliable. Myxozoans and *C. nodosus* were not common enough to be used as tags for deepwater redfish (1% and 2% prevalence overall, respectively). *Sphyrion lumpi* use redfish as its definitive host but only adult females are embedded permanently in the flesh, and sores of previous infections were taken into account in our study.

Larvae of *A. simplex* were common at almost all sites, but were particularly abundant off Labrador, on the Flemish Cap, and in the Gulf of St. Lawrence. The most prevalent and abundant parasite encountered was *H. aduncum* in redfish from the Flemish Cap. The copepod *S. lumpi* was most prevalent in the Gulf of St. Lawrence and the Laurentian Channel. Prevalence and mean intensity of these parasites are shown in Table 3.

Results of multiple nonparametric analyses demonstrated that at least one of the three parasite species differed in mean abundance between all adjacent areas, with the exception of the Labrador Sea and the Gulf of St. Lawrence. Mean abundance of both *H. aduncum* and *S. lumpi* in redfish from the Flemish Cap and the Cabot Strait–Laurentian Channel were significantly different (bootstrap adjusted $P<0.0001$ and 0.01, respectively). Mean abundance of *H. aduncum* also differed between fish from the Flemish Cap and the Labrador Sea (bootstrap adjusted $P<0.05$). Lastly, mean abundance of *A. simplex* differed between fish from the Gulf of St. Lawrence and those from the Cabot Strait–Laurentian Channel (bootstrap adjusted $P<0.01$) (Table 4).

Given that the Gulf of St. Lawrence (unit 1) and the Cabot Strait–Laurentian Channel (unit 2) populations are currently managed as separate stocks, we wished to validate our results. Analyses demonstrate that for *A. simplex*, mean abundance is significantly different in fish from unit 2 collected in winter and those from the Gulf of St. Lawrence (unit 1) collected in summer (bootstrap adjusted $P<0.05$), but no difference could be shown between those collected in winter versus summer from unit 2, nor between those collected in the summer compared to winter within the Cabot Strait–Laurentian Channel (Table 5).

Discussion

Criteria for the use of parasites as biological markers of fish populations have been reviewed by Williams et al. (1992). In this study, we employed the following four criteria for biological markers: geographic variation in prevalence or abundance, longevity of infection, absence of reproduction directly in or on the host, and ease of detection and enumeration. First, geographic variation in prevalence and abundance was observed in the various parasites. Second, the parasites or their remains have a

Table 4

Nonparametric length-stratified comparison of parasite mean abundance in redfish (*Sebastes mentella*) between management units. Winter and summer samples from unit 2 were pooled for these analyses. Overall test multiplicity is corrected for by bootstrap.

Parasite	Comparison	Raw *P*-value	Bootstrap *P*-value
Anisakis simplex	Flemish Cap and Labrador Sea	0.4941	0.9997
	Flemish Cap and unit 2	0.0083	0.0900
	Labrador Sea and unit 1	0.0184	0.1932
	unit 1 and unit 2	0.0008	0.0090*
Hysterothylacium aduncum	Flemish Cap and Labrador Sea	0.0014	0.0151*
	Flemish Cap and unit 2	<.0001	<0.0001*
	Labrador Sea and unit 1	0.1794	0.9039
	unit 1 and unit 2	0.1546	0.8629
Sphyrion lumpi	Flemish Cap and Labrador Sea	0.7774	1.0000
	Flemish Cap and unit 2	0.0006	0.0077*
	Labrador Sea and unit 1	0.3077	0.9872
	unit 1 and unit 2	0.0308	0.3065

Table 5

Nonparametric, length stratified comparison of parasite mean abundance in redfish (*Sebastes mentella*) between unit 1 (Gulf of St. Lawrence) and unit 2 (Cabot Strait–Laurentian Channel). Overall test multiplicity is corrected for by bootstrap.

Parasite	Comparison	Raw *P*-value	Bootstrap *P*-value
Anisakis simplex	unit 1(summer) and unit 2 (winter)	0.0042	0.0238*
	unit 2 (summer) and unit 2 (winter)	0.9150	1.0000
Hysterothylacium aduncum	unit 1(summer) and unit 2 (winter)	0.9050	1.0000
	unit 2 (summer) and unit 2 (winter)	0.1613	0.6454
Sphyrion lumpi	unit 1(summer) and unit 2 (winter)	0.4326	0.9653
	unit 2 (summer) and tunit 2 (winter)	0.4018	0.9517

long life span in their hosts. Larval anisakid nematodes can survive for a number of years in the fish host; McClelland and Marcogliese (1994) provided a detailed discussion of the use of anisakid parasites as biological tags for fish stocks. They pointed out that although prevalence and abundance of anisakids may vary over longer time scales, they are stable over the time frame (a few years) of a given survey, rendering them suitable for a stock discrimination study. Remarkably, of the 24 studies on biological tags reviewed by Arthur (1997) between 1990 and 1997, eight of them employed anisakid nematodes. Although the copepod *S. lumpi* has a limited life span, the cepahlothorax and scar tissue from previous infections persist for many years (Templeman and Squires, 1960; Sindermann, 1961; Reimer and Szuks, 1989; Bakay, 1988[1]). Third, none of these parasites multiply directly on the host and thus augment their abundance, as in the case of some protozoans and monogeneans. The anisakids are larval stages, and the copepod produces free-swimming larvae. Lastly, the parasites chosen are easily detected and counted.

We have shown that the parasite fauna of the deepwater redfish (*S. mentella*) can provide useful information on stock discrimination and definition of stock boundaries, as has been demonstrated for other fishes (see Williams et al. 1992; Arthur, 1997). Indeed, fish from all adjacent zones, with the exception of the Labrador Sea and Gulf of St. Lawrence, could be separated on the basis of abundance of at least one species of parasite. Distinction between redfish from the Gulf of St. Lawrence (unit 1) and the Cabot Strait–Laurentian Channel (unit 2) is reinforced by analyses demonstrating differences between the mean abundance of *A. simplex* in fish collected from the Gulf in summer and those in unit 2 in winter or summer. Furthermore, there were no differences in abundance of *A. simplex* detected in fish from unit 2 between winter and summer. Our results also support those of previous studies that demonstrated differences between redfish from the Flemish Cap and the Labrador Sea according to their parasite fauna (Templeman and Squires, 1960; Bourgeois and Ni, 1984). All areas sampled in our study are currently managed as separate stocks, and our results do not suggest that management strategies should change. However, the inclusion of Cabot Strait in unit 1 in the winter should be re-evaluated with further sampling.

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Our parasite results are in contrast with results using microsatellite DNA markers (Roques et al., 2002), in which *S. mentella* from the Gulf of St. Lawrence could not be differentiated from those of the Laurentian Channel. For this species, only three divergent populations were defined across the North Atlantic: 1) a western population in the Gulf of St. Lawrence and offshore Newfoundland; 2) a panoceanic population; and 3) an eastern population in Norway and the Barents Sea. Thus redfish from unit 1 could not be differentiated from those of unit 2. Similar results were reported for *S. fasciatus* sampled in units 1 and 2 (Roques et al., 2001). Redfish populations in both units are characterized by the presence of hybrid and introgressed individuals between *S. fasciatus* and *S. mentella* (Roques et al., 2001). Stock distinction does not preclude genetic exchange between stocks, but managers must be aware of the size and spatial boundaries of stocks, as well as the level of gene flow between the stocks.

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Dive-depth distribution of loggerhead (*Carretta carretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: Might deep longline sets catch fewer turtles?

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The Hawaii-based longline fishery operates over a large area in the central North Pacific, from the equator to latitude 45°N, between longitudes 130°W and 180°W. In 2000, 125 vessels were active in the fishery, producing total landings estimated at 24 million pounds and exvessel (wholesale) revenues of $50 million. The target species include bigeye tuna *(Thunnus obesus)*, yellowfin tuna (*T. albacares*), and albacore tuna (*T. alalunga*), and swordfish (*Xiphias gladius*).

Caught incidentally with these target species are leatherback (*Dermochelys coriacea*), loggerhead (*Carretta carretta*), olive ridley (*Lepidochelys olivacea*), and green (*Chelonia mydas*) sea turtles.

Over the period 1994–99, it was estimated that an annual average of 418 loggerhead, 112 leatherback, 146 olive ridley, and 40 green sea turtles were caught in the Hawaii-based longline fishery (McCracken[1]).

Historically, the Hawaii longline fishery has set longlines considerably shallower than 100 m to target swordfish (*Xiphias gladius*) or substantially deeper than 100 m to target bigeye tuna. Incidental hookings of loggerhead turtles have been reported in the Hawaii longline fishery observer data, which cover about 5% of the total annual effort. Analyses of these data found that loggerhead turtles were caught only when gear was set shallow enough to target swordfish, primarily in the northern portion of the fishing ground. No loggerhead sea turtles were caught when longline gear was set deep to target bigeye tuna, primarily in the southern portion of the fishing ground. These analyses suggest that a ban of shallow sets in the fishery since 1 April 2001 may reduce future incidental catches of loggerhead sea turtles. However, analyses based only on observer data suffer from the limited observer coverage and the dependence between depth of setting and area fished. For example, swordfish are targeted at night in the north, whereas tuna are targeted during the day in the south. To better understand the depths inhabited by sea turtles, we used diving depth distributions collected from satellite-linked dive recorders attached to two loggerhead and two olive ridley sea turtles caught and released in the Hawaii-based longline fishery. Although other studies on the dive depths of olive ridley and loggerhead sea turtles have been conducted in the Pacific, these have been conducted with sea turtles in coastal areas rather than in the oceanic central Pacific (Sakamoto et al., 1993; Beavers and Cassano, 1996).

Materials and methods

We attached Wildlife Computer Argos satellite-linked depth recorders (SDR-T10) to two loggerhead and two olive ridley sea turtles that had been caught with commercial longline fishing gear. One loggerhead and one olive ridley were hooked in the mouth and were released after the hook and line had been removed. The other loggerhead and olive ridley sea turtle had deeply ingested hooks, and for both of these turtles the fishing line was cut close to the mouth but the hook was not removed. Trained observers on the fishing vessel attached transmitters to the carapace of each of the four sea turtles, using fiberglass cloth strips and polyester resin patterned after the method presented in Balazs et al. (1996). The observers noted that all four sea turtles swam vigorously away after release.

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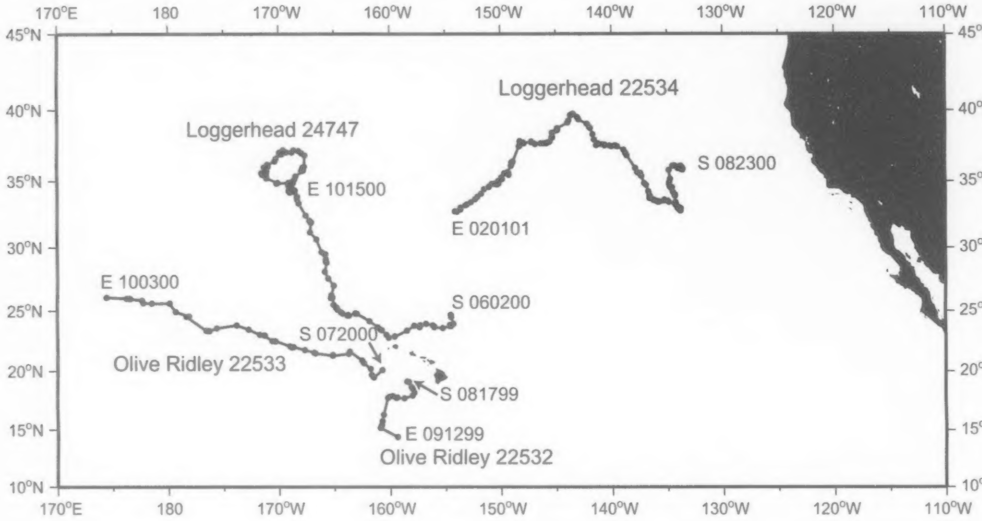

Figure 1

The start (S) and end (E) dates and track lines for the four turtles with satellite-linked dive recorders.

Data on daily location of the turtles were estimated from the signals received by the Argos receiver on a NOAA satellite. The position data were edited, and only the single most accurate daily position was plotted. The accuracy of each position was estimated by Argos as a function of the number and configuration of satellites and the number of transmissions received. Data on the dive behavior transmitted by the Argos receiver were not individual dive profiles but rather frequency distributions of time at depth, dive duration, and maximum dive depth, aggregated over four 6-hour periods and binned in specific depth or time intervals. The lower range of the depth bins (in meters) for the time-at-depth distributions were 1, 3, 5, 10, 15, 25, 35, 50, 60, 75, 100, 125, 150, 150+. Each time the turtle descended below 2 m, it was recorded as a dive. The lower range of the depth bins (in meters) for the dive-depth distributions were 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 100, 150, 150+. The 6-hour periods over which the time-at-depth and dive-depth data were pooled were programed in Hawaii standard time as 2100–0300, 0300–0900, 0900–1500, and 1500–2100 h. One period was night, another mid-day; one included dawn, the other dusk. Mean time-at-depth and dive-depth distributions for each turtle in each of the four time periods were computed as the average of all frequency distributions for each 6-hour period. Mean time-at-depth and dive-depth distribution for the combined four time periods for each species were computed as the average of the four mean time-at-depth and dive depth distributions for each turtle, then averaged by species.

Finally, after every 20 transmissions a special status message that contained technical data about the operation of the transmitter and the maximum dive depth of that day was transmitted. Both the loggerhead and the olive ridley sea turtles made some dives below 150 m; however, the histogram data did not indicate how much deeper than 150 m these animals dived. The maximum dives sent in the status messages were used to obtain some data on the deep dives.

Results

The positions of the four turtles showed that the turtles were occupying the characteristic habitats for each species: the loggerhead sea turtles were found in the northern portion of the subtropical gyre, and the olive ridley sea turtles were found farther south, well within the center of the subtropical gyre (Fig. 1). Loggerhead no. 24747, which was released with the hook removed, measured 83 cm (straight carapace length (SCL)) and transmitted data for 5.4 months. Loggerhead no. 22534, released with the hook deeply ingested, measured 61 cm SCL and transmitted data for 5.2 months. Olive ridley no. 22533, released with the hook deeply ingested, measured 57 cm SCL and transmitted data for 3.4 months. Olive ridley no. 22532, which was released after a hook was removed, measured 58 cm SCL and transmitted data for 0.8 months.

The time-at-depth frequency distributions for day and night periods for each of the sea turtles showed consistent diurnal and species differences in their dive-depth distributions (Fig. 2). The turtles spent more time at the surface during the day than at night and also dived deeper during the day (Fig. 2). We do not show the dive-depth distribution for the dawn and dusk periods, but these frequency distributions fell between the distribution for day and night periods.

Because it can often take as long as 20 hours to completely set and retrieve a longline, we examined time-at-

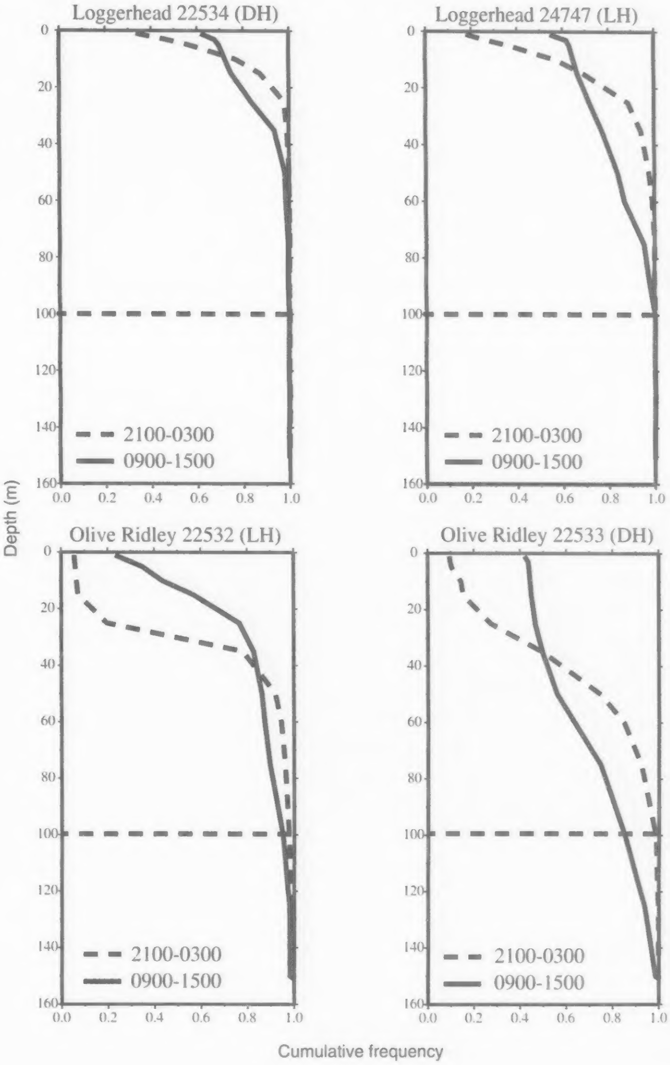

Figure 2

Time-at-depth cumulative frequency distributions for day (0900–1500 h) and night (2100–0300 h) periods for each of the four turtles. The 100 m reference depth is noted with a dashed line. DH indicates that the turtle was released with the hook deeply ingested, LH indicates that the turtle was lightly hooked and released with the hook removed.

depth and dive-depth distributions pooled over the four 6-hour time periods by species. The time-at-depth frequency distribution showed that the loggerhead sea turtles spent about 40% of their time in the top meter and virtually all their time shallower than 100 m (Fig. 3). We also examined the frequency distribution of the maximum depth of each dive and the deepest dive in a 24-hour period. The cumulative distribution of maximum depth of each dive indicated that most dives were very shallow: 70% of the dives were no deeper than 5 m (Fig. 3). The cumulative distribution of the maximum dive depth achieved over a 24-hour period indicated that for approximately 5% of the days, a dive exceeded 100 m (Fig. 3). Status messages reported that the deepest daily dive recorded was 178 m.

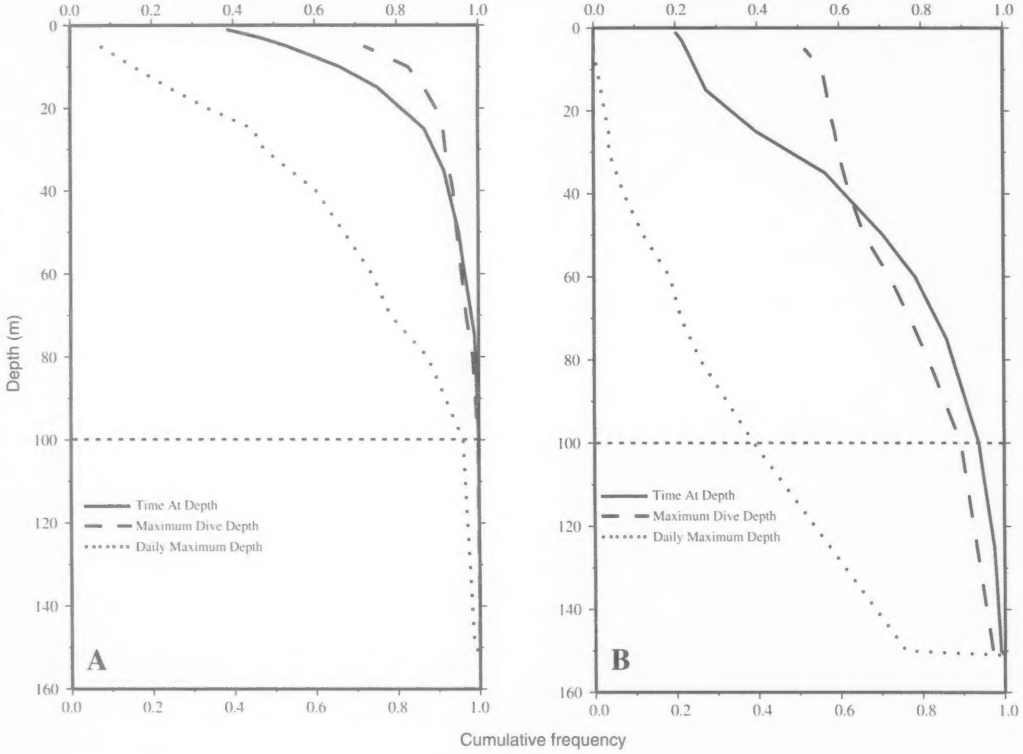

Figure 3

The time-at-depth, maximum dive depth, and daily maximum dive-depth cumulative frequency distributions for all periods combined: (**A**) the two loggerhead sea turtles combined; (**B**) the two olive ridley sea turtles combined.

By comparison, the time-at-depth and maximum depth-frequency distributions of the two olive ridley sea turtles showed considerably deeper depth distribution (Fig. 3). These sea turtles spent only about 20% of their time in the top meter and about 10% of their time deeper than 100 m (Fig. 3). Their daily maximum depth exceeded 150 m at least once in 20% of the days (Fig. 3). Status messages reported that daily dives of 200 m occurred—one dive recorded at 254 m.

Discussion

The loggerhead dive-depth distributions indicated that these animals tended to remain at shallower depths than that of 100 m. If shallow longline sets were replaced with deep longline sets, the incidental takes of loggerhead sea turtles should be reduced substantially. Further, even though olive ridley sea turtles dived deeper than loggerhead sea turtles, only about 10% of their time was spent deeper than 100 m. Therefore, their incidental catches should also be substantially reduced with the elimination of shallow longline sets. However, when deep sets are being made or retrieved or when current shear prevents the gear from sinking to its expected depth, hooks will be present in relatively shallow depths and could result in incidental catches of turtles.

Results to date in the fishery confirm the reduction in incidental catches of turtles that can be achieved from the elimination of shallow sets. Beginning in April 2001, shallow sets were prohibited in the Hawaii-based longline fishery. Data from the onboard observers in the longline fleet, which now comprise 20% of the fishing effort, showed that no loggerhead and only two olive ridley sea turtles were caught from April through December 2001.

The relatively shallow dive-depth distribution for loggerhead sea turtles in the central North Pacific is consistent with our understanding of their ecology; they forage and migrate along convergent fronts where they encounter a shallow aggregation of forage (Polovina et al., 2000). Although oceanic loggerhead sea turtles have a shallower dive behavior than that of olive ridley sea turtles, they appear to dive deeper in oceanic habitat than loggerhead sea turtles in coastal habitat. For example, the dive distribution of two loggerhead sea turtles between nesting periods off Japan indicated that virtually all their dives were shallower than 30 m (Sakamoto et al., 1993). The deeper-dive distribution of olive ridley sea turtles is also consistent with their oceanic habitat, which is south of the loggerhead habitat in the central portion of the subtropical gyre. The oceanography of this region is characterized by a warm surface layer, a deep thermocline depth, and an absence of strong horizontal temperature gradients and physical or biological fronts. It is likely that the deeper diving seen in the olive ridley sea turtles results from foraging at depths associated with the deep scattering layer.

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Age-validation of a leopard shark (*Triakis semifasciata*) recaptured after 20 years

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On 10 July 1999, vertebrae bearing an oxytetracycline (OTC) time mark were retrieved from a tagged leopard shark (*Triakis semifasciata*) recaptured in San Francisco Bay, CA, after being at liberty for almost 20 years. An additional long-term leopard shark tag return was received in June 2001, for which growth information (but not vertebrae) was obtained. The first recapture is significant in that it represents the longest at-liberty period for an age-validated (OTC-injected) shark, extends and completes age validation for this species, spanning all age classes up to its estimated average maximum age, and provides an example of the persistence of the OTC time mark in an elasmobranch at liberty for almost 20 years. The recaptured leopard shark made in 2001 also provides valuable information on long-term growth from time of release to time of recapture. Findings are documented here so that other researchers are aware that validation is complete for this species, to present pertinent evidence of considerable interannual variability in growth in this species, and to report observations on processing difficulties relating to the ephemeral nature of the 20-yr-old OTC mark.

Earlier results from the tagging study that led to these recaptures were published by Smith (1984), Smith and Abramson (1990), and Kusher et al. (1992). These authors concluded that one pair of vertebral growth bands (one opaque, one translucent) is produced each year in this species for the age classes they examined (up to 17 years). Opaque bands are deposited primarily in late spring and summer (mainly in August in the San Francisco Bay area); translucent bands, presumably representing minimum growth periods, are deposited primarily in late fall and winter (Kusher et al., 1992). Average annual growth of recaptured leopard sharks examined in these studies ranged from 0.0 cm per year to 4.0 cm per yr (mean of 2.14 cm per yr); centra grew proportionately to shark length over all size classes sampled.

The leopard shark occurs from Baja California, Mexico, to Oregon; maximum confirmed size is 180 cm TL (Kato et al., 1967), but fish over 146 cm TL are uncommon off central California (Herald et al., 1960; Kusher et al., 1992). Age and size at which females first reach maturity have been estimated at approximately 13 yr and 110 cm TL, respectively; the gestation period is estimated at 10–12 months; and parturition takes place in spring (April–May peak) in San Francisco Bay (Smith and Abramson 1990; Kusher et al. 1992).

Methods

The recaptured sharks were from a group of 948 leopard sharks tagged and released off Hunterís Point (37°44′N lat., 122°21′W long.) in South San Francisco Bay between 26 July and 13 September 1979. All were injected with oxytetracycline hydrochloride (OTC), tagged on the dorsal fin with yellow plastic livestock rototags, and released as described by Smith (1984).

The shark returned in 1999 was caught on 10 July off Oakland Airport in San Francisco Bay by a recreational angler fishing ~8 km east of the original release point. The fish was measured and the vertebrae removed and later frozen. In the laboratory, the vertebrae were sectioned and mounted as described by Smith (1984). Various vertebral section widths (from 0.4 mm to 1.3 mm wide) were tested to determine the best thickness for interpreting narrow band patterns near the centrum edge. The transverse sections were viewed illuminated alternately by ultraviolet UV (365 nm) and transmitted light. Micrographs were taken with a Leica DMLB microscope with a Diagnostic Instruments SPOT CCD (charged coupled device) digital camera coupled through a 0.6× phototube, multiplied by the ocular magnifications of 1, 5, and 10× to obtain a total magnification of 0.6, 3, and 6×. The three magnifications were evaluated for the best possible counting path. The images were then analyzed with Media Cybernetics Image Pro Plus image analysis software (Media Cybernetics, 1998), with which increments were enhanced with an edge-sharpening filter. After the application of the filter the images were evaluated and counts from the OTC mark to the margin were made. An annulus was defined as the distal edge of each translucent band in the corpus calcareum, at the distal edge of each band pair (e.g. Kusher et al. 1992; Branstetter and Stiles 1987 and

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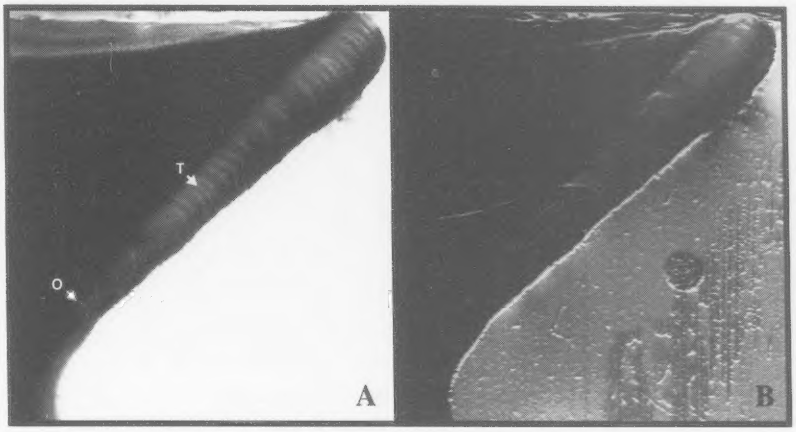

Figure 1

Photomicrographs of a transverse section of a vertebral centrum from a leopard shark (*Triakis semifasciata*) recaptured 10 July 1999 after ~20 years at liberty. (**A**) Transverse section viewed with transmitted white light showing broad dark opaque and narrow light translucent growth zones and ages up to year of tagging; and (**B**) the same section viewed with reflected ultraviolet light showing the OTC mark. 0 = first winter annulus, T = tagging and OTC injection of late summer 1979.

others). The first translucent band was interpreted as the first winter growth after parturition (year 0); the subsequent annulus interpreted as year 1. Band pairs distal to the tetracycline mark were compared with the number of years that the fish had been at liberty. For publication, digital photomicrographs were further enhanced to improve contrast and definition with Jasc Paintshop Pro software (Jasc Software, Inc., 1999).

Growth information for the other tagged fish (male, tag no. 337, recaptured in South San Francisco Bay on 9 June 2001) was obtained by comparing tagging and recapture size. Age and growth information for both recaptured sharks was compared with Kusher et al.'s (1992) von Bertanlanffy growth curves (their Figs. 4, 9, and 10) based on aged vertebrae from 1) fishery and market samples, and 2) earlier recaptures from the same 1979 tagging experiment.

Results

The shark recaptured in July 1999 was a mature female measuring 124 cm TL at recapture. At liberty growth and exact time at liberty could not be calculated because the tag number had worn away, preventing referral back to original tagging length and day. Because the one-time tagging experiment took place 26 July–13 September 1979, the fish had been at liberty from 19.8 to 19.9 years. The tetracycline mark was visible as a thin yellow line in all vertebral sections examined (Fig. 1). In less than a minute, the fluorescence began to decay rapidly, much more rapidly than tetracycline marks observed by the senior author in previous recaptured sharks (sharks at liberty 7 years or less). This fast decay made viewing of actual samples brief; most time was dedicated to setting up and taking digital photomicrographs of the sections.

Twenty annuli up to winter 1998 (including the 1979–80 winter annulus deposited after tagging) were visible distal to the time mark (Fig. 2), including a partially formed opaque band interpreted as the 1998 summer band (Fig. 3). We could not determine with any certainty whether the narrow opaque edge represented the beginning of the summer 1999 band (Fig. 3). On all sections examined, the last band pair at the centrum edge (i.e. the most recently deposited) was very narrow and faint, or incomplete and difficult to differentiate, especially on vertebral sections that were sliced too thick or too thin (best thickness was 0.6 mm). Proximal to the OTC mark were five annuli, indicating that the fish was 4+ yr old at tagging and was probably born in spring of 1974. The fish was aged as 24+ or in its 25th year. Width of the opaque bands indicative of annual summer growth was highly variable, although it generally tended to decrease with increasing age. Greatest relative growth in centrum diameter occurred in the first few years of life, and also in 1985, 1986, and 1987, judging from the width of the corresponding opaque zones (ages 11, 12, and 13). The recapture size (124 cm TL) was 11 cm smaller than that predicted for an age-25 female with the von Bertalanffy growth function (VBGF) generated by Kusher et al. (1992, their Fig. 4) for 162 untagged leopard sharks. But it was close to that predicted by their FISHPARM VBGF generated from band counts and lengths of tag recaptures from this same 1979 experiment (Kusher et al. 1992, their Fig. 10).

The other recaptured leopard shark (a male, no. 337) was caught 9 June 2001 in South San Francisco Bay off

San Mateo, CA, making a total of 120 recaptured leopard sharks from the original 1979 tagging. The tag number was readable and traceable back to the tagging date (23 August 1979) and length (87 cm TL), which was compared with the recapture length (119.4 cm TL) and date. This individual exhibited an average annual growth of only 1.47 cm/yr, but its recapture length for its presumed age (30) was also close to that predicted by the Kusher et al. (1992) asymptotic FISHPARM VBGF for tagged and recaptured leopard sharks.

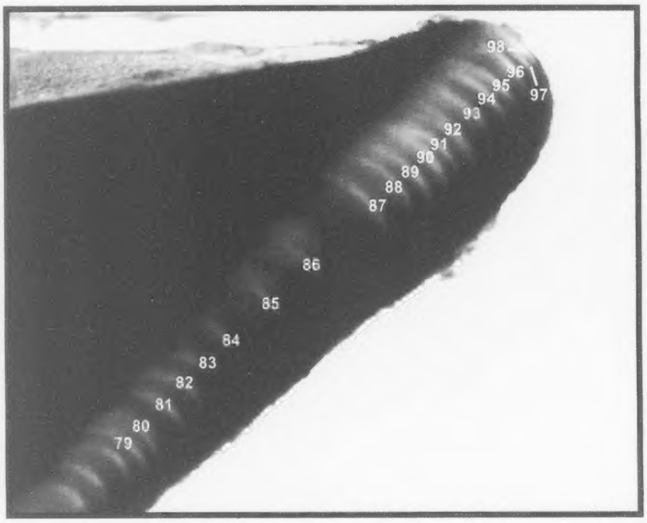

Figure 2

Enlargement of photomicrograph of a transverse vertebral section of a leopard shark (*Triakis semifasciata*) showing years (abbreviated in figure) that correspond to annuli distal to the tetracycline mark at year 1979 on the corpus calcareum.

Discussion

The tagging and recapture of fish whose calcified structures have been marked with the calcium-labeling fluorophor OTC offer a simple and conclusive method for establishing the timing of growth zone formation in these structures. Validating the timing of centrum or spine band formation is especially important for elasmobranchs as a group because, unlike teleosts, the assumption of annual deposition of band pairs has not been confirmed for many species and has been challenged for some. It has been suggested that two band pairs are deposited annually in the basking shark, *Cetorhinus maximus* (Parker and Stott, 1965) and the shortfin mako shark, *Isurus oxyrinchus* (Pratt and Casey, 1983), although validation is still pending for these species. Furthermore, Natanson (1984) and Natanson and Cailliet (1990), working with OTC-injected Pacific angel sharks, *Squatina californica*, found no correlation between centrum band deposition and any temporal cycle and concluded that bands were deposited in response to somatic growth. Nevertheless, elasmobranchs for which the deposition of one band pair per year has been established and validated with OTC (for at least selected size and age classes) include the thornback ray, *Raja clavata*, (Holden and Vince, 1973; Ryland and Ajayi, 1984); *R. microocellata* and *R. montagui* (Ryland and Ajayi, 1984); *Raja erinacea* (Natanson, 1993); *Bathyraja* sp. (Gallagher and Nolan, 1999); lemon shark, *Negaprion brevirostris* (Gruber and Stout, 1983; Brown and Gruber, 1988); spiny dogfish, *Squalus acanthias* (Beamish and McFarlane, 1985; Tucker 1985) leopard shark, *Triakis semifasciata* (Smith, 1984; Kusher et al., 1992); neonate sharpnose, *Rhizoprionodon terraenovae*, and sandbar, *C. plumbeus*, sharks (Branstetter 1987); and bonnethead shark, *Sphyrna tiburo* (Parsons 1993).

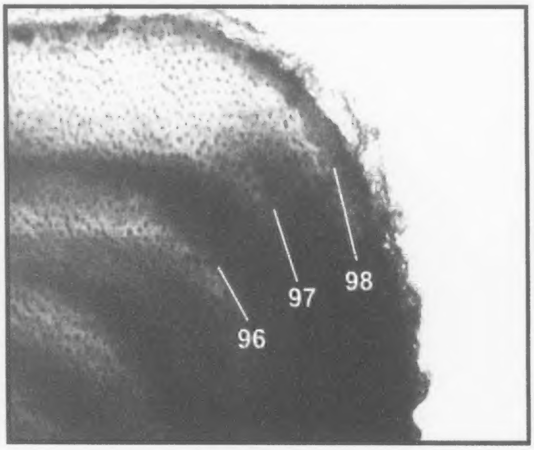

Figure 3

Enlarged view of the edge of the corpus calcareum of a transverse section of a leopard shark (*Triakis semifasciata*) vertebra, showing partially complete annuli at the centrum edge.

By demonstrating the persistence of OTC in the mineralized tissue of a cartilaginous fish at liberty for nearly two decades, our study confirms the long-term effectiveness of this age validation tool. The number of band pairs conformed to the number of years at liberty, although bands near the centrum periphery appeared in some sections to be absent or incompletely formed, even after careful embedding and sectioning. This emphasizes the importance of interpreting bands nearest the growing margin with extreme care, especially when examining band patterns in older, slow-growing sharks. For these fish, less precise preparation methods (such as examining whole centrum faces) are probably inadequate for interpreting narrow growth bands that form later in life. Additionally, in species like the leopard shark, the most recently deposited band pair may only become clearly defined or fully differentiated as new tissue after the accretion of subsequent bands. Thus, although most band pairs seem to be relatively well defined in this species (even in older specimens such as this one), the peripheral bands can be indistinct or incomplete. Beamish and McFarlane (2000), who recently reported on a sablefish (*Anoplopoma fimbria*) recaptured up to 20 years after being injected with OTC, also warned that the aging structures of long-lived fish require very careful preparation and interpretation.

In the vertebrae of the 1999 recaptured leopard shark, substantial centrum growth occurred in the late 1980s, e.g. the width of the 1987 growth zone (at 13 yr old) was over twice that of annual growth zones adjacent to it. We cannot explain why this period may have been so favorable for this shark over previous and subsequent years, but it does suggest that this species is capable of great interannual variability in growth, even at a relatively advanced age. Lenarz et al. (1995) described mild El Niño conditions off central California in 1987–88, although temperatures were less elevated than during other El Niño events, and only short periods of unusually high sea-level anomalies were observed. Moser et al. (2002) classified 1985–87 as a "normal" oceanographic period off California, between the warm 1982–83 El Niño episode and a cool-water 1988 La Niña episode.

OTC fluorescence is known to fade with exposure to UV light; therefore samples are traditionally stored in darkness and processed in dim light (Weber and Ridgeway 1962). The OTC mark in the leopard shark at liberty for 20 years was especially light-sensitive, disappearing after a few minutes exposure, much more quickly than tetracycline marks observed previously by one of the authors in earlier recaptures from this study. This may be due to diminishment of the phosphorescent properties of the chemical, combined with compression of the mark within the cartilage matrix over time. Therefore, when working with cartilaginous fishes (especially those at liberty for many years), it may be extremely important to obtain as many vertebrae as possible, to keep OTC-labeled centra away from light, to preplan microscope viewing sessions carefully, and to process and photograph samples quickly.

Previous studies have validated annual periodicity in leopard sharks up through age 17 (Smith 1984; Kusher et al. 1992). Beamish and McFarlane (1983) pointed out that band periodicity must be established for a full range of age classes to fully meet the requirement of age validation in fishes. This requirement is seldom met and has not yet been achieved for any elasmobranch. The OTC-labeled fish recaptured in 1999 measured 2 cm longer but was 8 years older than the oldest age-validated leopard shark of Kusher et al. (1992). This latter fish, also a female, measured 122 cm TL and was estimated to be 17 yr of age. It had been at liberty for 7.3 years—the longest duration recorded in that study. Results of the present study extend age validation for this species to fish at liberty for up to 19+ years, up to 124 cm TL, and up to 25 yr old. Longevity of this species has been estimated at 25–30 years (Smith, 1984); thus full validation for this species spanning ages 0 through 25 is now complete.

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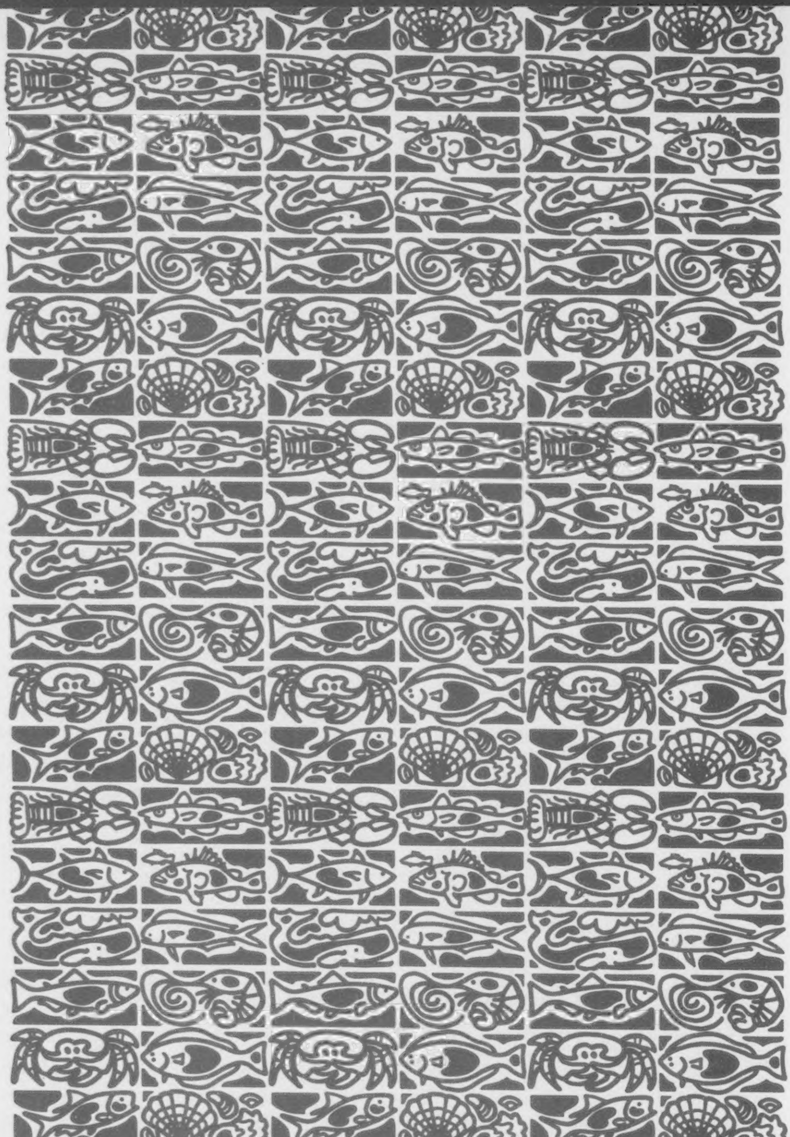Copies of published articles and notes are available free of charge to the senior author (50 copies) and to his or her laboratory (50 copies). Additional copies may be purchased in lots of 100 when the author receives page proofs.